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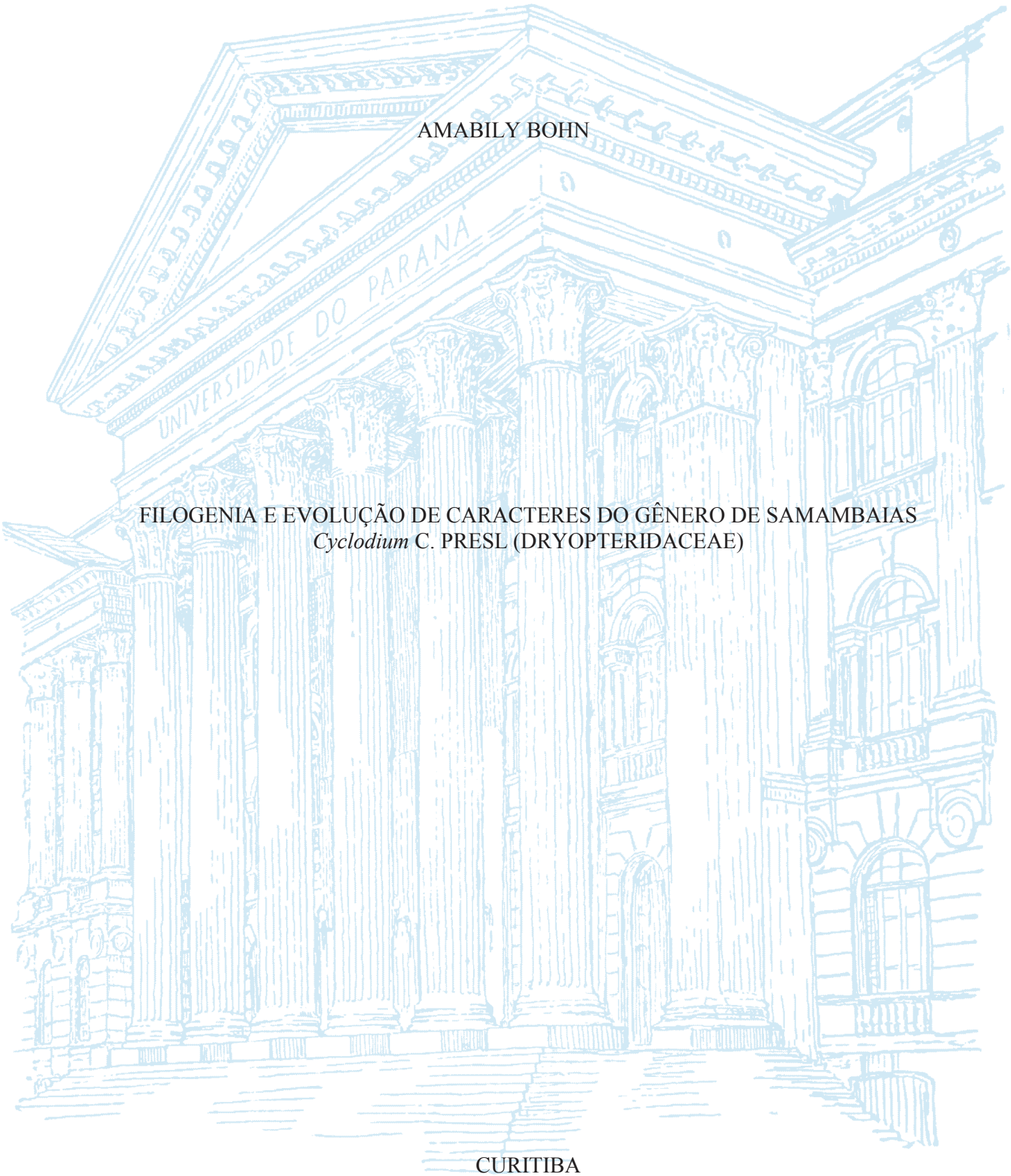

FILOGENIA E EVOLUÇÃO DE CARACTERES DO GÊNERO DE SAMAMBAIAS *Cyclodium* C. PRESL (DRYOPTERIDACEAE)

CURITIBA

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Dissertação apresentada ao curso de Pós-Graduação em Botânica, Setor de Ciências Biológicas, Universidade Federal do Paraná, como requisito parcial à obtenção do título de Mestre em Botânica.

Orientador: Prof.° Dr. Paulo H. Labiak Evangelista

Coorientador: Dr. Fernando Bittencourt Matos

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Filogenia e Evolução de Caracteres do gênero de samambaias *Cyclodium* C.Presl (Dryopteridaceae)

por

Amabily Bohn

Dissertação aprovada como requisito parcial para obtenção do grau de Mestre no Programa de Pós-Graduação em Botânica, pela Comissão formada pelos doutores

Paulo Henrique Labiak Evangelista

Renato Goldenberg

Duane Fernandes de Souza Lima

Curitiba, 28 de março de 2019.

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RESUMO

Cyclodium é um gênero de samambaias leptosporangiadas da família Dryopteridaceae, caracterizado morfologicamente por suas frondes férteis e estéreis geralmente dimorfas, soros arredondados, e indúsios peltados. A maioria das espécies é terrestre e sua distribuição é exclusivamente neotropical, ocorrendo desde o Panamá e Trindade até a Argentina, Paraguai e sudeste do Brasil. *Cyclodium* pertence ao clado das samambaias polibotrióides, composto principalmente por plantas hemiepifíticas e com frondes dimorfas. Os objetivos deste trabalho são investigar as relações filogenéticas das espécies de *Cyclodium* e do gênero com outros grupos de Dryopteridaceae, a evolução de 12 caracteres morfológicos e do hábito, além de atualizar a taxonomia para o gênero. A análise filogenética foi conduzida através de cinco sequências de DNA cloroplastidial (*rbcL, rps4-trnS, trnG-trnR, psbA-trnH* e *trnP-petG*), utilizado os métodos Bayesiano e de Máxima Verossimilhança. A análise incluiu 24 terminais de *Cyclodium* (78% das espécies e variedades anteriormente descritas por Smith). Os resultados demonstram que *Cyclodium* é monofilético e grupo irmão de *Polybotrya*. Além disto, *C. calophyllum, C. heterodon, C. inerme, C. meniscioides, C. trianae* var. *trianae* e *C. trianae* var. *chocoense* são monofiléticas. Quatro caracteres morfológicos foram úteis para suportar a monofilia de alguns grupos: indúsio peltado para o gênero; a ausência de escamas na face abaxial da costa para *C. alansmithii* e *C. inerme*; esporos com a perina perfurada para *C. heterodon, C. alansmithii, C. inerme, C. akawaiorum, C. meniscioides, C. calophyllum, C. guianense,* and *C. rheophilum,* e reverte para não perfurado em *C. guianense* e *C. inerme*; dimorfismo das frondes férteis e estéreis e ápice conforme para *C. akawaiorum* e *C. meniscioides.* Na revisão do gênero, reconhecemos 13 espécies de *Cyclodium*, considerando as novidades taxonômicas que foram propostas como as espécies novas *C. alansmithii* e *C. pubescens*, a mudança de status de variedade para espécie da variedade de *C. trianae,* e a união das variedades de *C. heterodon* e *C. meniscioides* no táxon de origem. Foram designados lectótipos para *C. calophyllum*, *C. guianense* e *C. meniscioides.*

Palavras-chave: Biodiversidade. Neotrópico. Polibotrióides. Samambaias.

ABSTRACT

Cyclodium is a leptosporangiate fern genus that belongs to Dryopteridaceae, morphologically characterized by its usually dimorphic fertile-sterile fronds, round sori, and peltate indusia. Most of species are terrestrial and it is exclusively neotropical, occurring from Panama and Trinidad to Argentina, Paraguay, and southeastern Brazil. *Cyclodium* belongs to the polybotryoid clade, which is mostly represented by hemiepiphytic plants with dimorphic fronds. The goals of this study are to investigate the phylogenetic relationships among *Cyclodium* species and between the genus with other groups of Dryopteridaceae, the character evolution of 12 morphological characters, and growth habit, besides to update the taxonomy of the genus. The phylogeny was built using five cloroplastidial DNA (*rbcL, rps4-trnS, trnG-trnR, psbA-trnH,* and *trnP-petG*), under the Maximum Likelihood and Bayesian methods. The analysis included 24 *Cyclodium* terminals (78% of species and varieties previously described by Smith). The results show that the genus is monophyletic and sister to *Polybotrya*. Furthermore, *C. calophyllum, C. heterodon, C. inerme, C. meniscioides, C. trianae* var. *trianae* and *C. trianae* var. *chocoense* are monophyletic. Four morphoplogical characters were useful to support the monophyly of certain groups: peltate indusium for *Cyclodium*; the absence of scales on costae abaxially for *C. alansmithii* and *C. inerme;* perforated perine of spores for *C. heterodon, C. alansmithii, C. inerme, C. akawaiorum, C. meniscioides, C. calophyllum, C. guianense,* and *C. rheophilum,* whitch reverts to non-perforated in *C. guianense* and *C. inerme;* sterile-fertile fronds dimorphism and conform apex for *C. akawaiorum* and *C. meniscioides.* On the genus revision, we recognized 13 species of *Cyclodium*, including the taxonomic novelties proposed, as the new species *C. alansmithii* and *C. pubescens*, the variety *C. trianae* raising status to species, and the lumping of the varieties of *C. heterodon* and *C. meniscioides* in the autonymic taxon. Lectotypes were designated to *C. calophyllum*, *C. guianense* and *C. meniscioides.*

Key-words: Biodiversity. Neotropics. Polybotryoids. Ferns.

SUMÁRIO

1 INTRODUÇÃO GERAL

Dryopteridaceae Herter é uma família de samambaias da subordem Polipodiineae, composta por 3 subfamílias, 26 gêneros e aproximadamente 2115 espécies (PPG I, 2016). Dentro de Dryopteridaceae, destaca-se o clado das samambaias polibotrióides, caracterizado por plantas geralmente hemiepífitas e com dimorfismo foliar acentuado entre frondes férteis e estéreis (MORAN e LABIAK, 2015). Este clado corresponde à subfamília Polybotryoideae H.M.Liu & X.C.Zhang, a qual contém sete gêneros e aproximadamente 100 espécies (PPG I, 2016).

Cyclodium C. Presl destaca-se como o terceiro maior gênero da subfamília Polybotryoideae (PPG I, 2016). A história taxonômica de *Cyclodium* pode ser considerada relativamente curta, se comparada com a de outros gêneros de Dryopteridaceae. O gênero foi descrito pela primeira vez pelo botânico checo Karel Borivoj Presl, que admitiu apenas três espécies (PRESL, 1836): *Cyclodium confertum* (*Aspidium confertum* Kaulf.), *C. glandulosum* (*A. glandulosum* Blume), e *C. meniscioides* (*A. meniscioides* Willd.). Nos anos subsequentes, as mudanças taxonômicas mais expressivas foram de Hooker (1862) e Hooker e Baker (1867), que trataram *Cyclodium* como pertencente à *Aspidium* Sw., e Kuntze (1891) e Morton (1939), que sinonimizaram o gênero em *Dryopteris* Adans. Christensen (1913; 1920) incluiu espécies subgrupos de *Dryopteris* e *Polystichopsis*, que mais tarde foram considerados como integrantes de *Cyclodium*: *Dryopteris guianensis* (Klotzsch) Posth e *D. sancti-gabrieli* (Hook.) Kuntze (=*C. guianense* (Klotzsch) van der Werff ex L.G.D.Gómez), e *D. varians* (Fée) Kuntze (=*C. varians* (Fée) A.R.Sm.) em *Dryopteris* subg. *Stigmatopteris* grupo *Peltochlaena*, além de *Dryopteris trianae* (Mett) Kuntze (=*Cyclodium trianae* (Mett.) A.R.Sm.) em um subgrupo de *Polystichopsis.*

O estudo taxonômico mais recente e compreensivo para o gênero foi apresentado por Smith (1986), que envolveu análises taxonômicas, anatômicas e biogeográficas. Neste estudo foram reconhecidas dez espécies, além de duas variedades de *C. meniscioides* (Willd.) C. Presl, uma de *C. heterodon* (Schrad.) T. Moore e uma de *C. trianae*. Apesar de não haverem tratamentos taxonômicos expressivos recentes, o gênero foi incluído em diversas floras e listas de espécies regionais, como Cremers et al (1993) para as Guianas, Smith & Moran (1995) para a Mesoamérica, Mori et al (1997) para a Guiana Francesa, Murillo-Pulido et al (2008) para a Colômbia e Bohn et al (2019) para o Brasil. Estudos recentes de filogenia molecular demonstraram que *Cyclodium* é monofilético, grupo irmão de *Polybotrya* e pertencente ao clado polibotrióde (SCHUETTPELZ e PRYER, 2007; MORAN e LABIAK,

2015; LIU et al, 2016; MORAN e LABIAK, 2016).

As principais características morfológicas do gênero são rizomas dictiostélicos, grande número de feixes vasculares na base do pecíolo, frondes 1 a 2-pinadas (raramente simples ou mais divididas), raques com sulcos adaxiais mais ou menos contínuos com as pinnas, lâminas cartáceas a subcoriáceas, soros arredondados com indúsios geralmente peltados, esporos monoletes e bilaterais com a perina dobrada e equinulada, e $x = 41$. A presença de indúsio peltado é considerada uma das mais distintas e diagnósticas para *Cyclodium*, além da ausência de tricomas aciculares sobre a lâmina (SMITH, 1986).

Todas as espécies tem distribuição Neotropical, ocorrendo principalmente nas montanhas ao redor da bacia amazônica (Andes e região do Maciço das Guianas), mas com registros também em Trinidad, Panamá, na bacia amazônica, na Floresta Atlântica brasileira (desde o Ceará até São Paulo), além do norte do Paraguai e Argentina (SMITH, 1986; BOHN et al., 2019). O centro de diversidade é nas Guianas, onde seis das dez espécies ocorrem, além de quase todos os híbridos naturais de *Cyclodium*. Os locais úmidos parecem ser preferidos pelas espécies deste gênero e a maioria delas é encontrada em altitudes entre 0-800 metros (SMITH, 1986). A maioria das espécies é terrestre, condição considerada ancestral dentro do gênero (MORAN e LABIAK, 2015), mas algumas também apresentam comportamento epifítico, hemiepifítico, epipétrico e reofítico (SMITH, 1986). Além de alguns híbridos naturais citados por Smith (1986), dois novos híbridos entre *Cyclodium* e *Polybotrya* foram descritos recentemente, um no sudeste da Amazônia – ×*Cyclobotrya telespirensis* Engels e Canestraro (ENGELS e CANESTRARO, 2017) e outro no Ceará - ×*Cyclobotrya amalgamata* Schwartsb. & Canestraro (SCHWARTSBURD et al, 2018). A presença destes híbridos, é um indicativo de que o processo de hibridização parece ser importante para a diversificação das espécies de *Cyclodium*.

Considerando que os aspectos do hábito, características morfológicas e distribuição geográfica de *Cyclodium* são únicos dentro do clado das polibotrióides, o gênero é um modelo ideal para que algumas hipóteses evolutivas sejam testadas. Ademais, os trabalhos mais recentes que envolvem *Cyclodium* não são específicos sobre o gênero. Deste modo, o presente trabalho utilizou dados moleculares e ferramentas modernas de análises comparativas para se responder algumas questões básicas sobre a evolução em *Cyclodium*, e utilizour estes resultados para embasar uma nova proposta taxonômica para o gênero.

A seguir, apresentamos 3 capítulos com os resultados obtidos durante o desenvolvimento da dissertação. No capítulo 1, os resultados da filogenia e evolução do

hábito e caracteres morfológicos são apresentados e discutidos. No capítulo 2, propomos uma nova espécie e uma mudança de status, com base na filogenia e taxonomia. Por fim, no capítulo 3, apresentamos uma revisão taxonômica atualizada para o gênero.

2 METODOLOGIA

2.1 ESTUDOS TAXONÔMICOS

Foram examinadas cerca de 686 espécimes dos seguintes herbários: CAY, INPA, MBM, NY, P, RB, RON, UC, UFP, UPCB and US. Imagens de materiais dos herbários BHCB, C, COL, F, HUA, JOI, K e PACA foram utilizadas. Os tipos foram examinados nos herbários B, BM, BR, C, COL, GH, INPA, K, NY, MICH, MO, P, UC, UEC e US, e através de imagens *online* disponíveis no site *JSTOR Global Plants*. É apresentada uma lista de espécimes examinados. Para evitar a citação de um grande número de representantes para a mesma região, apenas um espécime por município (ou divisão política equivalente) foi selecionado. A lista de coletores está disponível no Apêndice 1 (Capítulo 3) e inclui todos os materiais examinados para este estudo.

Para as descrições morfológicas, as medidas de comprimento e largura foram obtidas a partir da maior folha de cada espécime. Os tricomas e escamas foram medidos com o auxílio de um estereomicroscópio AmScope SM-3TX, no Laboratório de Pteridologia, no Departamento de Botânica, da Universidade Federal do Paraná, Brasil. As imagens de tricomas, escamas, protoescamas e indúsio foram feitas com um estereomicroscópio LEICA MZ16, com uma câmera fotográfica acoplada (LEICA DFC 500) na Coleção Entomológica Padre Jesus Santiago Moure, no Departamento de Zoologia da Universidade Federal do Paraná, Brasil. Imagens de Microscopia Eletrônica de Varredura foram tomadas para análise da ornamentação do perisporo, esporângios e tricomas. Os materiais foram transferidos com agulhas para *stubs* de alumínio cobertos com asfalto adesivo. Os *stubs* foram cobertos com ouro por 2 minutos e os esporos foram digitalmente fotografados utilizando o microscópio eletrônico de varredura JEOL JEM 1200EX-II, no Centro de Microscopia Eletrônica da Universidade Federal do Paraná, Brasil.

Informações acerca da distribuição geográfica foram obtidas das etiquetas e convertidas com a ferramenta Conversor do SpLink, quando necessário (http://splink.cria.org.br/conversor). Os mapas de distribuição foram feitos com o software QGIS 3.2.0 (QUANTUM GIS DEVELOPMENT TEAM, 2013). As camadas foram construídas com arquivos *raster* (1:10,000,000) do Natural Earth (www.naturalearthdata.com)

e arquivos *shape* (unidades políticas e rios) obtidos da Organization for Flora Neotropica (www.nybgpress.org). O status de conservação foi calculado com a ferramenta GeoCAT (Bachman et al, 2011), considerando as células com 2 km de largura. Os resultados da análise foram discutidos de acordo com a IUCN Red List categories and criteria (IUCN, 2001).

2.2 ANÁLISES MOLECULARES

Com relação às análises moleculares, a amostragem do grupo externo incluiu os quatro gêneros do clado polibotrióide (*Maxonia* C.Chr.*, Olfersia* Raddi*, Polybotrya* Humb. & Bonpl. ex Willd. E *Polystichopsis* (J.Sm.) Holttum), com a adição de gêneros pertencentes às subfamílias Dryopteridoideae B.K.Nayar, Elaphoglossoideae (Pic.Serm.) J.P.Roux e *Lomariopsis* Fée (Lomariopsidaceae Alston) (Tabela 2, Capítulo 2). A amostragem de *Cyclodium* foi definida de acordo com as buscas preliminares em herbários e no campo. Após estudar diversos espécimes de diferentes herbários, selecionamos representantes de todas as espécies e variedades reconhecidas por Smith (1986), assim como outros grupos morfológicos ainda não nomeados. Quando possível, foram utilizados mais de um espécime por espécie de *Cyclodium*, para testar a monofilia dos táxons e diminuir o erro por problemas de extração, PCR e sequenciamento.

DNA plastidial foi extraído de material de herbário ou tecido ressecado em gel de sílica. Extrações foram feitas utilizando o mini-kit Qiagen DNeasy *plant* (Valencia, CA) seguindo o protocolo do fabricante (espécimes de herbário sofreram um passo adicional, sendo incubados em 42ºC por 12 horas com o *buffer* de lise). Todos os marcadores (*rbcL, rps4-trnS, trnG-trnR*, *psbA-trnH* e *trnP-petG)* foram amplificados por PCR em um volume total de 15 μL de acordo com o protocolo usado por Labiak e Moran (2017). A programação da PCR para o *rbcL* e o *trnG-trnR* consistiu em 5 minutos de desnaturação em 94°C, 35 ciclos de 1 minuto em 94°C, 1 minuto em 50°C, 2.5 minutos em 72°C e 10 minutos de período de extensão em 72°C. Para os demais marcadores, a programação utilizada consistiu em 5 minutos de desnaturação em 94°C, 35 ciclos de 1 minuto em 94°C, 30 segundos em 50°C, 1 minuto em 72°C e 7 minutos de período de extensão em 72°C (LABIAK e MORAN, 2017). Géis de agarose 1% revelados em brometo de etídio foram utilizados para testar os produtos da amplificação. As extrações e PCR foram realizados pelo Programa de Sistemática Molecular Lewis B. and Dorothy Cullman do Jardim Botânico de Nova Iorque.

Para o *rbcL*, os *primers* utilizados foram ESRBCL1F e ESRBCL1361R (SCHUETTPELZ e PRYER, 2007), para *rps4-trnS* os *primers* rps4-3r.f (SKOG et al, 2004) e

trnSr (SOUZA-CHIES et al, 1997), para *trnG-trnR* os *primers* TRNG1F e TRNR22R (NAGALINGUM et al, 2007), para *psbA-trnH* os *primers* $trnH^{GUG}$ (TATE e SIMPSON, 2003) e psbA (SANG et al, 1997) e para *trnP-petG* os *primers* $trnP^{UGG}$ e petG2 (SMALL et al, 2005). Para o sequenciamento, utilizamos os mesmos *primers* de amplificação, mais os ESRBCL628F e ESRBCL654R para o *rbcL* (SCHUETTPELZ E PRYER 2007), e os 43F1 e 63R f para o *trnG-trnR* (NAGALINGUM et al. 2007).

Todos os produtos da PCR foram sequenciados pela Macrogen-USA. As sequências resultantes foram editadas usando o programa Geneious 9 (Biomatters, Auckland, NZ). As novas sequências consenso obtidas foram submetidas para o GenBank.

2.3 ALINHAMENTO E ANÁLISES FILOGENÉTICAS

As sequências de consenso foram alinhadas com o Muscle v. 3.8.31 (EDGAR, 2004) e o alinhamento resultante foi manualmente alterado quando necessário no Mesquite v. 3.40 (MADDISON & MADDISON, 2018). Os melhores modelos evolutivos para cada região foram obtidos através do Critério de Informação Akaike (Akaike Information Criterion - AIC) e o Critério de Informação Bayesiano (Bayesian Information Criterion – BIC) utilizando o programa jModeltest2 v. 2.1.10 (DARRIBA et al, 2012; GUINDON & GASCUEL, 2003) (Tabela 1, Capítulo 2).

As análises Bayesianas (BI) foram realizadas através do programa Mr. Bayes 3.2.2 (RONQUIST e HUELSENBECK, 2003) na plataforma CIPRES (MILLER et al, 2010). Os modelos utilizados foram GTR+I+G para o marcador *rbcL* e GTR+G para os demais marcadores. Os parâmetros escolhidos para a análise foram: três corridas, cada uma com 20 milhões de gerações, com uma amostragem a cada 1000 gerações. Utilizamos as parcelas de likelihood (In*L*) no programa Tracer v.1.6 (RAMBAUT e DRUMMOND, 2013), para identificar a qualidade da corrida e se a simulação de Monte Carlo via cadeia de Markov (MCMC) alcançou estabilidade. O suporte dos ramos foi estimado através dos valores de Probabilidade Posterior (PP) obtidos através da análise MCMC e as árvores foram editadas no programa FigTree (http://tree.bio.ed.ac.uk/software/figtree/). As análises de Máxima Verossimilhança (ML) foram realizadas utilizando o programa RAxML-HPC Black x (STAMATAKIS, 2014) na plataforma CIPRES (MILLER et al, 2010). Foi selecionada a opção ML+*thorough bootstrap*, utilizando o modelo GTR+G para todos os marcadores. O suporte dos ramos (ML-BS) foi estimado através de 1000 réplicas de *bootstrap*.

2.4 EVOLUÇÃO DE CARACTERES MORFOLÓGICOS

As informações de hábito e caracteres morfológicos de *Cyclodium* e grupo exteno foram obtidas a partir dos espécimes de herbário e, quando necessário, de tratamentos taxonômicos ou imagens disponíveis nos sites JSTOR (https://plants.jstor.org/), e PlantSystematics (http://www.plantsystematics.org/). Foram obtidos treze caracteres (Table 1 – Capítulo 1), optimizados nas árvores de geradas com a análise de Máxima Verossimilhança a partir dos dados moleculares. A matriz foi construída no programa Mesquite v. 3.40 (MADDISON e MADDISON, 2018), e analisada através do critério de Máxima Parcimônia. Apenas um espécime por espécie foi mantido, para simplificar a árvore gerada.

Para observar a perina dos esporos de *Cyclodium,* foram feitas imagens de microscopia eletrônica de verredura com o JEOL JSM-6360LV no Centro de Microscopia Eletrônica da Universidade Federal do Paraná. Os esporos foram transferidos com agulhas de espécimes de herbário para *stubs* de alumínio cobertos com adesivo asfáltico, que posteriormente foram cobertos com ouro durante dois minutos.

CAPÍTULO 1 – Phylogeny and Character Evolution of the Neotropical Fern Genus *Cyclodium* (Dryopteridaceae)

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Phylogeny and Character Evolution of *Cyclodium*

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Abstract We performed a molecular phylogenetic analysis for *Cyclodium* using the plastidial markers *rbcL*, *rps4-trnS, trnG-trnR, psbA-trnH* and *trnP-petG*, under the Bayesian and Maximum Likelihood methods. We optimized onto the resulting tree 12 morphological characters and growth habit. Our results support *Cyclodium* as monophyletic and sister to *Polybotrya*, as has been recovered by previous studies. *Cyclodium* is further supported as monophyletic by the synapomorphies of terrestrial habit, monomorphic sterile and fertile leaves, and peltate indusia. Within *Cyclodium*, *C. trianae* var. *chocoense* and *C. trianae* var. *trianae* form a clade sister to the rest of the genus. They differ from their congeners by 2-pinnate-pinnatifid or more divided leaves, which represent a retention of the ancestral character of the outgroups. Our results also provide evidence for some taxonomic novelties within the genus, such as the recognition of the two varieties of *Cyclodium trianae* at species rank, and the lumping of the two varieties of *C. heterodon* into a single taxon.

Keywords biodiversity-evolution-polybotryoids-systematics

Cyclodium C. Presl belongs to Dryopteridaceae Herter, a monophyletic family of extant leptosporangiate ferns that comprises three subfamilies, 26 genera, and about 2,115 species (PPGI, 2016). Presl (1836) originally described the genus and classified three species in it. The only comprehensive monograph of the genus is that of Smith (1986). He recognized 10 species, of which three were assigned a total of four varieties (not counting the autonymic type variety): Thus, Smith (1986) recognized 14 taxa (species and varieties), and this number has been unchanged to the present.

Geographically, *Cyclodium* is entirely Neotropical, occurring in Panama, Trinidad, French Guiana, Suriname, Guyana, Venezuela, Colombia, Ecuador, Peru, Bolivia, Paraguay, northern Argentina, and Brazil (Smith, 1986; Bohn et al., 2019) (Fig. 1). The Guiana region is its center of diversity, harboring seven of the 14 taxa—more than any other region in the Neotropics. It is also the region where almost all of the genus's natural hybrids are found (Smith, 1986).

Wet, shaded forests, from 0–800 m, are the typical habitat for *Cyclodium*. Most of the species are terrestrial, a condition that optimizes as plesiomorphic for the genus (Moran & Labiak, 2015). Some species have been recorded as being either rooted climbers (occurring in the soil and with long-creeping rhizomes climbing when encountering trunks), epipetric, or rheophytic (Smith, 1986). *Cyclodium* does not contain hemiepiphytes in the strict sense, because none of its species establish as gametophytes on the bases of trees and then, after fertilization, produce a climbing rhizome with long feeding roots extending to the soil. This growth habit, now well documented in ferns (Nitta & Epps, 2009; Lagomarsino et al., 2012; Testo & Sundue, 2014; Canestraro et al., 2014; Labiak et al., 2017), has not been found in *Cyclodium*.

Morphologically, Smith (1986) characterized *Cyclodium* by a suite of characters, the most important being dictyostelic rhizomes, numerous vascular bundles in stipe bases, the grooves of the rachis open to admit the pinna-grooves, bilateral spores with a folded perine, and $x = 41$. Based on these characters, Smith (1986) suggested that *Cyclodium* was a dryopteroid genus related to *Polybotrya* Humb. & Bonpl. ex Willd., *Maxonia* C.Chr., and *Olfersia* Raddi. This similarity was further discussed by Moran (1987), who considered as shared traits amongst these genera to be 1) dimorphism of the sterile and fertile fronds, 2) creeping rhizomes, 3) tendency for root-climbing habit, 4) anastomosing venation, and 5) the more dissected lamina (as in *C. trianae*).

Another genus once thought related to *Cyclodium* is *Stigmatopteris* C. Chr. (Christensen, 1913, 1920; Tryon & Tryon, 1982). This was based on leaf cutting, absence of

hairs on the laminae, and similarities in venation pattern (Moran, 1991b). Nevertheless, *Stigmatopteris* was considered by Smith (1986) to be more distantly related, differing by the absence of indusia, presence of pellucid-punctate glands in lamina, serrate pinna apices, thin laminae, and veins ending in a clavate tip (hydathodes) before the segment margins.

Molecular phylogenetic studies have supported the monophyly of *Cyclodium* and its more distant relationship to *Stigmatopteris* within the Dryopteridaceae. Instead, these studies suggest that *Cyclodium* is sister to *Polybotrya,* and that these two genera form a clade with *Maxonia*, *Olfersia,* and *Polystichopsis* (J. Sm.) Holttum, and two neotropical species most closely related to *Olfersia* but currently classified in *Arachniodes* Blume (Schuettpelz & Pryer, 2007; Moran & Labiak, 2015, 2016). Members of this clade typically have a root-climbing growth habit, long-creeping rhizomes, and (except *Polystichopsis*) dimorphic sterile and fertile fronds. The clade has been informally called the "polybotryoid clade" by Moran & Labiak (2015). Subsequently, Liu et al. (2016) found that *Trichoneuron* Ching, a monotypic Asian genus, to be sister to *Polystichopsis*, and they proposed the informal name "polystichopsioids" to refer to the clade formed by these two genera. The name was considered useful because the two genera have monomorphic sterile and fertile fronds, unlike the four dimorphic genera in the polybotryoids.

Most of the previous molecular phylogenetic studies that have included *Cyclodium* have sampled only one species (Schuettpelz & Pryer, 2007; Liu et al., 2016; Moran & Labiak, 2016). So far, the most comprehensive phylogenetic study of the genus is that of Moran & Labiak (2015), which included six species. Because their study focused on *Polybotrya*, the evolution of growth habits and morphological characters in *Cyclodium* was not thoroughly explored.

The purpose of the present article is to provide a comprehensive molecular phylogeny for *Cyclodium* and use it to answer several questions about the genus's monophyly and relationships to other members of the polybotryoid clade; the monophyly of its species and varieties; the evolution of certain morphological characters that have been traditionally used in the taxonomy of the genus; and finally, to investigate the evolution of growth habits within the polybotryoid clade.

1. Material and methods

1.1 Taxonomic sampling

We included several outgroup taxa in our analyses (Appendix I). *Lomariopsis* Fée was included because it belongs to the Lomariopsidaceae, one of six families of eupolypods I that forms a clade sister to the Dryopteridaceae, the family to which *Cyclodium* belongs (Schuettpelz & Pryer, 2007; Labiak et al., 2014; Liu et al., 2016). The other outgroups were subfamilies of the Dryopteridaceae: Dryopteridoideae Link (five genera), Elaphoglossoideae (Pic. Serm.) Crabbe, Jermy & Mickel (seven genera), and Polybotryoideae H. M. Liu & X. C. Zhang (eight genera) (subfamilies according to PPG I, 2016). These groups were included because they cover most of the clades that have been recovered within the Dryopteridaceae (Schuettpelz & Pryer, 2007; Moran & Labiak, 2015; Liu et al., 2016). From the polybotryoid clade (sensu Moran & Labiak, 2015) to which *Cyclodium* belongs, all five remaining genera in that clade were included in the analyses (*Maxonia, Olfersia,* and *Polybotrya*), including two species currently classified in *Arachniodes* but known to be sister to *Olfersia* (Moran & Labiak, 2015). The two genera of the polystichopsiod clade, *Polystichopsis* and *Trichoneuron,* were also included as outgroups.

For the in-group, we included 24 specimens of *Cyclodium* (Appendix 1) representing eight of the species and two of the varieties (*C. trianae* var. *chocoense* and *C. heterodon* var. *abbreviatum*) recognized by Smith (1986).

1.2 DNA extraction

DNA was isolated from either field-collected, silica gel-dried fronds, or herbarium specimens. Total genomic DNA was extracted using the Qiagen DNeasy Plant Mini Kit (Valencia, CA) following the manufacturer's protocol. We used an additional step where the herbarium samples were incubated with the lysis buffer on a tipping plate at 42° for 12 hours.

1.3 PCR amplification and sequence generation

We sequenced five plastid markers: one gene (*rbcL*), and four non-coding intergenic spacers (*rps4-trnS, trnG-trnR, psbA-trnH,* and *trnP-petG*). Amplifications were made by PCR in 15 μL reactions according to the protocol cited by Labiak & Moran (2017). PCR program

for *rbcL* and *trnG-trnR* consisted in 5 min of initial desnaturation at 94°C, 35 cycles of 1 min at 94°C, 1 min at 50°C, 2.5 min at 72°C, and 10 min of extension period at 72°C. PCR program for *rps4-trnS, psbA-trnH* and *trnP-petG* consisted in 5 min of initial desnaturation at 94°C, 35 cycles of 1 min at 94°C, 30 s at 50°C, 1 min at 72°C and 7 min of extension period at 72°C (Labiak & Moran 2017). The final products of PCR were checked on a 1% agarose gel with ethidium bromide. The extractions and PCR analyses were made in the Program of Molecular Systematics Lewis B. and Dorothy Cullman of New York Botanical Garden.

For *rbcL*, we used the primers "ESRBCL1F" and "ESRBCL1361R" (Schuettpelz & Pryer 2007); for *rps4-trnS* the primers "rps4-3r.f" (Skog et al., 2004) and "trnSr" (Souza-Chies et al., 1997); for *trnG-trnR* the primers "TRNG1F" and "TRNR22R" (Nagalingum et al., 2007); for *psbA-trnH* the primers "trnH^{GUG}" (Tate & Simpson, 2003) and "psbA" (Sang et al., 1997); and for *trnP-petG* the primers "trnP^{UGG}" and "petG2" (Small et al., 2005). For sequencing, we used the amplification primers plus the internal "ESRBCL628F" and "ESRBCL654R" for *rbcL* (Schuettpelz & Pryer, 2007); and "43F1" and "63R" for *trnG-trnR* (Nagalingum et al., 2007). All PCR products were sequenced by Macrogen-USA. The resulting sequences were assembled using Geneious 9 (Biomatters, Auckland, NZ), and all newly obtained consensus sequences were submitted to GenBank (Appendix I).

1.4 Alignment and phylogenetic analyses

Consensus sequences were aligned using Muscle v3.8.31 (Edgar, 2004), and the resulting alignment was manually revised, when necessary, in Mesquite v. 3.40 (Maddison & Maddison, 2018). The best performing evolutionary models were obtained under the Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) using the program jModeltest2 version 2.1.6 (Darriba et al., 2012; Guindon & Gascuel, 2003).

Bayesian analyses (BI) were performed using Mr. Bayes 3.2.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003) in the CIPRES plataform (Miller et al., 2010). The evolutionary models were GTR+I+G for *rbcL* and GTR+G for the others, as suggested by jModeltest. The analyses were set to two runs and four chains, with 20 million generations, sampling every 1000th generation. To examine the quality of runs and to assess whether Markov Chain Monte Carlo (MCMC) reached stationarity, the loglikelihood (InL) plots were examined using the program Tracer 1.6 (Rambaut & Drummond, 2013). Branch support was estimated using the posterior probability (PP) values from the MCMC analysis, and trees were edited with the program Mesquite v. 3.40 (Maddison & Maddison, 2018).

Maximum Likelihood analyses (ML) were performed using the RAxML-HPC BlackBox 8.2.10 (Stamatakis, 2014) of CIPRES platform (Miller et al., 2010). We used the option ML + thorough bootstrap (ML-BS), using the GTR+G model for all markers. Branch supports (ML-BS) were estimated through 1000 bootstrap replicates.

1.5 Morphological data

For *Cyclodium* and the outgroups, morphological characters and growth habit were scored from herbarium specimens and, when necessary, general taxonomic treatments or images available on JSTOR (https://plants.jstor.org/), and PlantSystematics.org (http://www.plantsystematics.org/). Thirteen characters were scored (Table 1) and their states optimized onto the tree generated from the ML analysis of the molecular dataset. The matrix was generated in Mesquite v. 3.40 (Maddison & Maddison, 2018), and analyzed under Maximum Parsimony criterion.

To score perine characters, SEM images were digitally obtained using a JEOL JSM-6360LV scanning electron microscope at the Electron Microscopy Center at the Universidade Federal do Paraná. The spores were transferred with dissecting needles from herbarium specimens to aluminum stubs coated with asphalt adhesive, and these were sputter-coated with gold for two minutes.

2 Results

The combined matrix with the five plastid markers included 56 samples, of which 24 represent eleven taxa of *Cyclodium* (78.6% of the species and varieties in the genus), and 32 are outgroups. Six species and two varieties (not counting the autonymic type variety) could be tested for monophyly because we had two or more accessions: *Cyclodium calophyllum* (2), *C. guianense* (4), *C. heterodon* var. *heterodon* (2), *C. heterodon* var. *abbreviatum* (2), *C. inerme* (2), *C. meniscioides* var. *meniscioides* (3), *C. trianae* var. *trianae* (3), and *C. trianae* var. *chocoense* (3). The new species *Cyclodium alansmithii* Bohn & Labiak, was described in another article (Bohn et al., in press.) based on one specimen (*Tillet 44942*) of these analyses. The species was originally identified as *C. inerme,* and recovered as sister to *C. inerme,* but some of its morphological characters can be used to distinguish them as different species. Statistics for the molecular data, including number of sequences per marker, number of sites, and substitution models used in BI and ML analysis are summarized in Table 2.

The results of our BI and ML (Fig. 2) analyses support the monophyly of both the polybotryoid (PP = 1.0, ML-BS = 100%) and polystichopsioid clades (PP = 1.0, ML-BS = 100%). These two groups formed a clade recovered as monophyletic (PP = 1.0, ML-BS = 94%) and sister to a clade with members of subfamily Dryopteridoideae and *Stigmatopteris* (PP = 0.79, ML-BS = 48%). Subfamily Elaphoglossoideae was recovered as monophyletic (PP = 1.0, ML-BS = 100%), and sister to Dryopteridoideae + *Stigmatopteris* (PP = 0.63, ML-BS = 34%).

Cyclodium was resolved as monophyletic (PP = 1.0, ML-BS = 100%) and sister to *Polybotrya* (PP = 0.97, ML-BS = 66%). Also, the other polybotryoid genera were supported as monophyletic: *Maxonia* (PP = 1.0, ML-BS = 100%), *Olfersia* (PP = 1.0, ML-BS = 100%), and *Polybotrya* (PP = 1.0, ML-BS = 100%). Two neotropical species currently classified in *Arachniodes* (*A. ochropteroides* (Baker) Lellinger and *A. macrostegia* (Hook.) R.M.Tryon & D.S.Conant) did not form a clade with other species of *Arachniodes*. Instead, they formed a clade with *Olfersia* (PP = 0.81, ML-BS = 57%). The monotypic *Maxonia* formed a clade with *Polybotrya* and *Cyclodium* (PP = 1.0, ML-BS = 91%) (Fig. 2).

Within *Cyclodium,* the two varieties of *C. trianae* (Mett.) A.R.Sm. (sensu Smith, 1986) formed a clade (PP = 1.0, ML-BS = 88%) and each was recovered as monophyletic: var. *chocoense* (PP = 1.0, ML-BS = 99%) and var. *C. trianae* (PP = 1.0, ML-BS = 87%). *Cyclodium heterodon* was recovered as monophyletic (PP = 1.0, ML-BS = 89%); however, the relationships among its varieties from different geographical regions are not clearly resolved. All samples of *C. inerme* (Fée) A.R.Sm. also formed a clade (PP = 0.59, ML-BS = 100%), and this clade was sister to *C. alansmithii* Bohn & Labiak (PP = 1.0, ML-BS = 100%) (Fig. 2). The single specimen of *C. akawaiorum* A.R.Sm. was recovered in a clade with *C. meniscioides* (PP = 1.0, ML-BS = 100%). The three specimens of *C. meniscioides* var. *meniscioides* also formed a clade (PP = 1.0, ML-BS = 98%). Two Brazilian specimens of *C. meniscioides* var. *meniscioides* from Espírito Santo and Mato Grosso do Sul (*Labiak 4059*, and *Lehnard 36*) were resolved as monophyletic (PP = 1.0, ML = 98%) and sister to another specimen of *C. meniscioides* var. *meniscioides* from Ecuador (*Moran 3577*; PP = 1.0, ML-BS = 98%). *Cyclodium calophyllum* (C.V.Morton) A.R.Sm. is monophyletic (PP = 0.85, ML-BS = 95%) and sister to a clade with *C. guianense* (Klotzsch) A.R.Sm., and *C. rheophilum* A.R.Sm. (PP = 1.0, ML-BS = 100%). The relationships within this last clade were unresolved in our analysis (Fig. 2).

The evolution of the growth habit and morphological characters are shown in Figures 3, 4, 5 and 6. The densely echinulated spore surface was useful for defining the polybotryoid

clade, and the peltate indusium for *Cyclodium*. Some synapomorphies were found within the species of the genus: the absence of scales on costae abaxially to *C. alansmithii* and *C.* inerme, dimorphic sterile and fertile fronds, and conform laminar apex to *C. akawaiorum* and *C. meniscioides.* Most of the morphological characters used in this study were homoplastic within the polybotryoids or Dryopteridaceae.

3 Discussion

The results support the relationships of the subfamilies within Dryopteridaceae that were recovered by previous studies (Schuettpelz & Pryer, 2007; Moran & Labiak, 2015, 2016; Liu et al., 2016). The only exception was *Stigmatopteris,* whose relationship has varied in different studies (Fig. 2). Schuettpelz & Pryer (2007) recovered *Stigmatopteris* as sister to subfamily Elaphoglossoideae, whereas Liu et al. (2016) recovered it as a member of subfamily Polybotryoideae (a hypothesis adopted by PPGI, 2016). In our analysis, *Stigmatopteris* was recovered as sister to a large clade comprising *Dryopteris* Adans.*, Arachniodes, Phanerophlebia* C.Presl*, Cyrtomium* C.Presl, and *Polystichum* Roth. (Fig. 2). This agrees with results found by Moran & Labiak (2015, 2016). Although this relationship was well supported by the BI (PP = 1.0), it is only moderately supported by the ML analysis (ML-BS = 86%). Additional molecular markers are still needed to resolve the phylogenetic placement of *Stigmatopteris*.

3.1 The polybotryoid clade

The polybotryoid and polystichopsioid clades were recovered as monophyletic, and the relationships among their genera agree with those found by Moran & Labiak (2015) and Liu et al. (2016). As suggested by Liu et al. (2016), the polybotryoids (*Maxonia, Olfersia, Polybotrya,* and *Cyclodium*) and the polystichopsioids (*Polystichopsis,* and *Trichoneuron*) (Fig. 2) form two sister clades. Besides molecular evidence, the morphological recognition of the polystichopsioids is supported by the presence of pluricellular hairs on costae and rachis, monomorphic sterile and fertile fronds, and terrestrial habit (Liu et al., 2016).

We recovered a close relationship between *Olfersia* and two species currently classified in *Arachniodes* (*A. macrostegia* and *A. ochropteroides*) (Fig. 2), thus confirming the results of Moran & Labiak (2015) and Lu et al. (2018). As discussed by these authors, *Arachniodes s.s*. does not belongs to the polybotryoid ferns. To preserve monophyly, these

two species need to be placed in either *Olfersia* or a new genus. No known morphological synapomorphy supports the relationship between *Olfersia* and these two species.

For the polybotryoid ferns, discrete sori optimize as the plesiomorphic state (Fig. 5). It occurs in many of the outgroups and in the polybotryoid genera *Arachniodes, Cyclodium,* and *Maxonia.* Acrostichoid sori are homoplastic, having evolved twice within the polybotryoids: once in *Olfersia* and again in *Polybotrya*. The presence of indusia is the ancestral condition within the polybotryoid ferns, being present in *Arachniodes, Maxonia,* and *Cyclodium*, but with two losses in *Polybotrya* and *Olfersia*. This corresponds to the acrostichoid condition found in these genera (Fig. 5); no fern with acrostichoid sori has indusia (pers. obs.).

The evolution of growth habit within the polybotryoid ferns was previously discussed by Moran & Labiak (2015), and our results are similar to theirs. The terrestrial habit is plesiomorphic within the polybotryoids, and is present in most of the outgroups in the analyses. Nevertheless, the root-climbing habit (long-creeping rhizomes in the soil that climb by roots after encountering a trunk) has been important role in many clades, having evolved independently at least six times within the clade of *Maxonia, Polybotrya,* and *Cyclodium* (Fig. 3). Some species of *Cyclodium* are often recorded as epipetric and are frequent in creek beds (*C. alansmithii*, and *C. guianense*). This habit evolved independently four times within *Cyclodium*; namely, in *C. alansmithii, C. inerme, C. guianense*, and *C. rheophilum* (Fig. 3). Based on our results, it seems that the evolution of the root-climbing habit cannot be considered as a synapomorphy for polybotryioid clade.

The perines in the polybotryoid ferns are typical of many Dryopteridaceae. They are fabaeform, monolete, with elongate-continuous inflated folds, and perine lacking perforations (Smith, 1986; Moran et al., 2007; Moran et al., 2010a; Moran et al. 2010b; Labiak et al., 2014; Moran & Labiak, 2015), which are the ancestral conditions for the polybotryoids. According to our analyses, the densely echinulate perine is a synapomorphy to the polybotryoid ferns, although it is also present in other genera in the Dryopteridaceae: *Polystichopsis chaerophylloides* (Poir.) C.V.Morton*, Polystichum munitum* (Kaulf.) C.Presl*, Dryopteris wallichiana* (Spreng.) Hyl., and *Mickelia scandens* (Raddi) R.C.Moran, Labiak & Sundue (Fig. 6).

3.2 The *Cyclodium* clade

Our analyses support the monophyly of *Cyclodium,* a result recovered by previous

studies (Schuettpelz & Pryer, 2007; Moran & Labiak, 2015; Liu et al., 2016; Moran & Labiak, 2016). Peltate indusia optimize as a synapomorphy for the genus (Fig. 5). Several plesiomorphic characters are helpful to identify *Cyclodium*: the generally terrestrial habit; monomorphic sterile and fertile fronds (these two with an ambiguous ancestral condition); presence of scales on costae abaxially; generally 1-pinnate laminae with pinnatifid apices; and discrete round sori (Figs. 3, 4, and 5).

Of the eight (out of 14) taxa of *Cyclodium* tested for monophyly, four species (*C. calophyllum, C. inerme, C. meniscioides* var. *meniscioides* and *C. trianae* var. *trianae*) and one variety (*C. trianae* var. *chocoense*) were recovered as monophyletic. *Cyclodium guianense* was not resolved by BI analysis and formed a polytomy with *C. rheophilum.*

Creeping rhizomes are plesiomorphic within the Dryopteridaceae and were present in all species of polystichopsioid and polybotryoids ferns in our study (Fig. 3). Monomorphic sterile and fertile fronds (Fig. 3) and pinnatifid apices (Fig. 4) are the ancestral states in *Cyclodium*, but with two reversals to dimorphic fronds and conform apex in *C. akawaiorum* and *C. meniscioides* var. *meniscioides*. This indicates a close relationship of these species. *Cyclodium calophyllum* has a transitional state as regards dimorphism of sterile and fertile laminae, and we consider it here as subdimorphic (Fig. 3). Regarding laminar division, almost all the species of *Cyclodium* have 1-pinnate laminae except *C. trianae* var. *chocoense* and *C. trianae* var. *trianae,* which have 1-pinnate-pinnatisect to more divided laminae (Fig. 4). The two varieties of *C. trianae* are sister to the rest of *Cyclodium,* and their laminar division represents the retained ancestral character state in the polybotryoid ferns.

Indument characters have often been used to distinguish species of polybotryoid ferns (e.g., Smith, 1986; Moran, 1987, 1991b; Prado & Moran, 2015). Although *Cyclodium* bears short, spreading, yellowish or hyaline hairs, and scattered, uniseriate, brownish microscales on costa abaxially (Smith, 1986), we found no indument character state defining clades within the genus. The only exception is the clade comprising *Cyclodium alansmithii* and *C. inerme*, which lacks scales (Fig. 4) and has inconspicuous hairs and microscales on the costae.

Free venation is a plesiomorphic condition in *Cyclodium*, with at least three changes to the anastomosing condition within the genus (Fig. 3). Smith (1986) suggested that anastomosing veins seem to occur when fronds are less dissected, with some variation between species but, in *Cyclodium,* always following the same meniscioid pattern. According to our results, anastomosing venation evolved independently within *Cyclodium*, occurring in both 1-pinnate and more divided species (e.g., *C. calophyllym, C. heterodon*), and apparently

it is not related to the degree of laminar dissection.

Regarding indusial attachment in *Cyclodium,* Smith (1986) claimed that orbicular-reniform indusia with a narrow sinus was the ancestral condition, and that this state occurred in *C. trianae* and *C. seemannii* (Hook.) A.R.Sm. Reexamining these two species, we have noticed that there is a continuum between completely round, peltate indusium, to the reniform condition, even in the same specimen. It is easy to misinterpret this character because the indusia fold upwards and inward during maturation of the sporangia, making it difficult to detect the type of attachment. In all species of *Cyclodium*, however, we consider the type of indusial attachment as peltate, which is a synapomorphy for the genus according to our optimization of the character (Fig. 5).

Within *Cyclodium*, spore characters can be useful to distinguish certain clades or species. For instance, the perforation of the perine optimizes as a synapomorphy for *C. heterodon, C. alansmithii, C. inerme, C. akawaiorum, C. meniscioides* var. *meniscioides, C. calophyllum, C. guianense,* and *C. rheophilum.* The character reverses to non-perforate in *C. inerme* and *C. guianense.* The two varieties of *Cyclodium trianae* have different perines: *C. trianae* var. *trianae* has perforated perine, whereas *C. trianae* var. *chocoense* has non-perforated perine. The only species of *Cyclodium* with perine lacking broad folds is *C. rheophilum* (Fig. 6).

Our results support most of the species and varieties proposed by Smith (1986), but there were a few exceptions. One of them concerns the two varieties of *Cyclodium heterodon.* Smith (1986) distinguished them based on differences in venation and cutting of laminae (one pair of united veins and pinnatifid pinnae in *C. heterodon* var. *abbreviatum*, and 2–3 pairs of united veins and sinuate pinnae in the autonymic type variety). We found these characters to be variable, with intermediates distributed throughout the distribution of *C. heterodon* (Fig. 7). In our analysis, *C. heterodon* was recovered as monophyletic, but its two varieties were not (Fig. 2). Neither morphology nor geography distinguishes the two varieties. Taxonomically, we would recognize only *C. heterodon*, without varieties.

Smith (1986) distinguished two varieties of *Cyclodium trianae*: *C. trianae* var. *chocoense* and *C. trianae* var. *trianae*. The former differed by 1-pinnate-pinnatifid (vs. 2-pinnate-pinnatifid) fronds and its occurrence in the Pacific coast (Chocó region) of Colombia (vs. Amazonian Ecuador and Peru). Our results support the recognition of two clades, which can be treated either as varieties or even different species (Fig 2). Besides molecular evidence, we found non-perforated perine in *C. trianae* var. *chocoense* and perforated ones in *C. trianae* var. *trianae* (Fig. 6). Geographically, both varieties are distinct, with *C. trianae* var. *trianae*

occurring on the eastern side of the Andes and *C. trianae* var. *chocoense* on the western side (Smith, 1986). This geographic separation between sister species has been reported for other fern genera, such as *Alsophila* R.Br. (Moran, 1995), *Asplenium* L. (Murakami & Moran, 1993), *Bolbitis* Schott (Moran, 2016), *Cyathea* Sm. (Moran, 1991a), *Solanopteris* Copel. (which is now nested in *Microgramma* C.Presl; Moran, 1992), *Stigmatopteris* (Moran & Labiak, 2016), and *Trichomanes* (Moran, 1995). Given the morphological differences, geographical separation, and evidence of two clades from molecular phylogenetic studies (Fig. 2), we prefer to recognize the two varieties of *C. trianae* at species rank and plan to make the new combination (Bohn et al., in press.).

Another species in which Smith (1986) recognized varieties is *Cyclodium meniscioides*. Of the three varieties he recognized of this species, only *C. meniscioides* var. *meniscioides* was included in our analysis. It was recovered as monophyletic, but our sampling (only three specimens) is too limited to fully understand the morphological and genetic variation among the different populations of this widely distributed species. On the basis of morphology, Smith (1986) proposed that *C. meniscioides* var. *meniscioides* was related to *C. akawaiorum*. These two taxa were resolved as sister in our analysis (Fig. 2), supporting Smith's (1986) hypothesis. The relationship is also supported by the synapomorphies of strongly dimorphic (fertile-sterile) fronds, and conform terminal pinnae (Figs. 3, 4).

Cyclodium calophyllum, which had only two samples in our analysis, was resolved as monophyletic. It formed a well-supported clade (PP = 0.85, ML-BS = 95) along with *C. guianense* and *C. rheophilum* (Fig. 2). No morphological synapomorphy is known to support this clade. *Cyclodium guianense* and *C. rheophilum* were resolved as sister species (Fig. 2). Smith (1986) indicated similarities between *C. rheophilum* and *C. guianense*, but also thought *C. inerme* was related, which was not corroborated by our results.

Hybrids have been postulated between *Cyclodium* and *Polybotrya*, its sister genus. Several putative and poorly known intrageneric hybrids were pointed out by Smith (1986) on the basis of morphology. All came from the Guianan region. Little can be said about their origin and parentage until they can be studied in the field. Two intergeneric well documented hybrids between *Cyclodium* and *Polybotrya* have been found from Brazil. ×*Cyclobotrya telespirensis* Engels & Canestraro is a putative hybrid between *Cyclodium meniscioides* var. *meniscioides* and *Polybotrya goyazensis* Brade (Engels & Canestraro, 2017). Later, Schwartsburd et al. (2018) described ×*Cyclobotrya amalgamata* Schwartsb. & Canestraro, between *C. meniscioides* var. *meniscioides* and *P. osmundacea* Willd. The existence of these

taxa suggests that hybrids within *Cyclodium* probably occur and should be looked for in the field.

Unlike most fern genera, *Cyclodium* has both a modern monograph (Smith, 1986) and phylogenetic study (Moran & Labiak, 2015). However, we have very little chromosomal information on either the species or putative hybrids. Cytological studies might shed light on the possible occurrence of hybridization and polyploidy in the genus, two important evolutionary mechanisms for ferns in general, but phenomena not yet documented in *Cyclodium*.

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Table 1 List of characters and their states optimized onto our phylogenetic tree.

Character	States
Growth habit	Terrestrial (0); terrestrial root climber (1); epipetric (2);
Rhizome	erect or decumbent (0); creeping (1);
Sterile-fertile frond dimorphism	Monomorphic (0); dimorphic (1); subdimorphic (2);
Venation	Free (0); anastomosing (1);
Laminar division	Simple (0); 1-pinnate (1); 1-pinnate-pinnatisect (2); 2-pinnate or more divided (3);
Laminar apex	Conform (0); pinnatifid (1); not applicable (2); subconform (3);
Scales on costae abaxially	Absent (0); present (1);
Soral shape	Discrete (0); acrostichoid (1);
Indusia	Absent (0); present (1);
Indusial attachment	Attached at a sinus (0); peltate (1); not applicable (2);
Perine surface	Smooth (0); sparsely echinulate (1); densely echinulate (2); papillate (3); spiny (4);
Perine folds	Interrupted (0); elongate-continuous (1); absent (2);
Perine perforation	Absent (0); present (1);

Table 2 Number of sequenced taxa, character statistics, and evolutionary models for *rbcL* gene, and *rps4-trnS, trnG-trnR, psbA-trnH,* and *trnP-petG* intergenic spacers for *Cyclodium* and outgroups.

	rbcL	*rps4-trnS*	*trnG-trnR*	*psbA-trnH*	*trnP-petG*	Total
Total number of taxa (ingroup only)	15	23	13	26	20	—
Number of sites (indels included)	1287	493	1072	445	631	3928
Evolutionary models AIC/BIC	GTR+I+G/ SYM+I+G	GTR+G/ TPM1uf+G	GTR+G/ TPM1uf+G	GTR+G/ TPM1+G	TPM1uf+G/ TPM1uf+G	—
Number of variable sites	351	321	509	111	275	1567
PICs	232	206	347	60	165	1010

Fig. 1. Distribution and species richness in Neotropics (two-degree square) of *Cyclodium*.

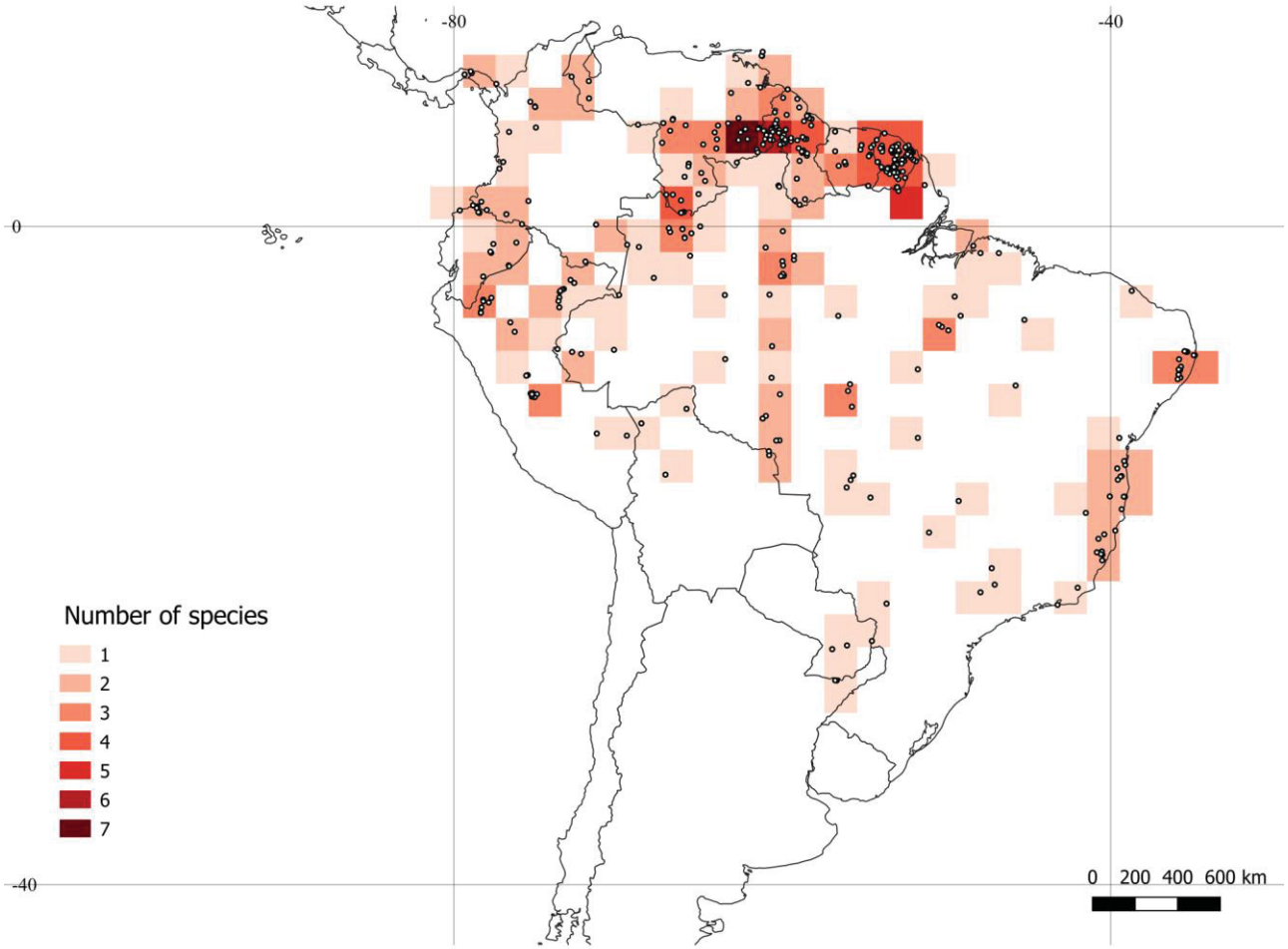


Fig. 2. Fifty percent majority-rule cladogram from the Bayesian analysis (left), and phylogram from the Maximum Likelihood analysis (right) of the combined cpDNA dataset (*rbcL, rps4-trnS, trnG-trnR, psbA-trnH,* and *trnP-petG*). Numbers above the branches represent the posterior probability values from the Bayesian analysis, and numbers below the branches represent the bootstrap values from the Maximum Likelihood analysis. In both analyses, the thick lines represent full support.

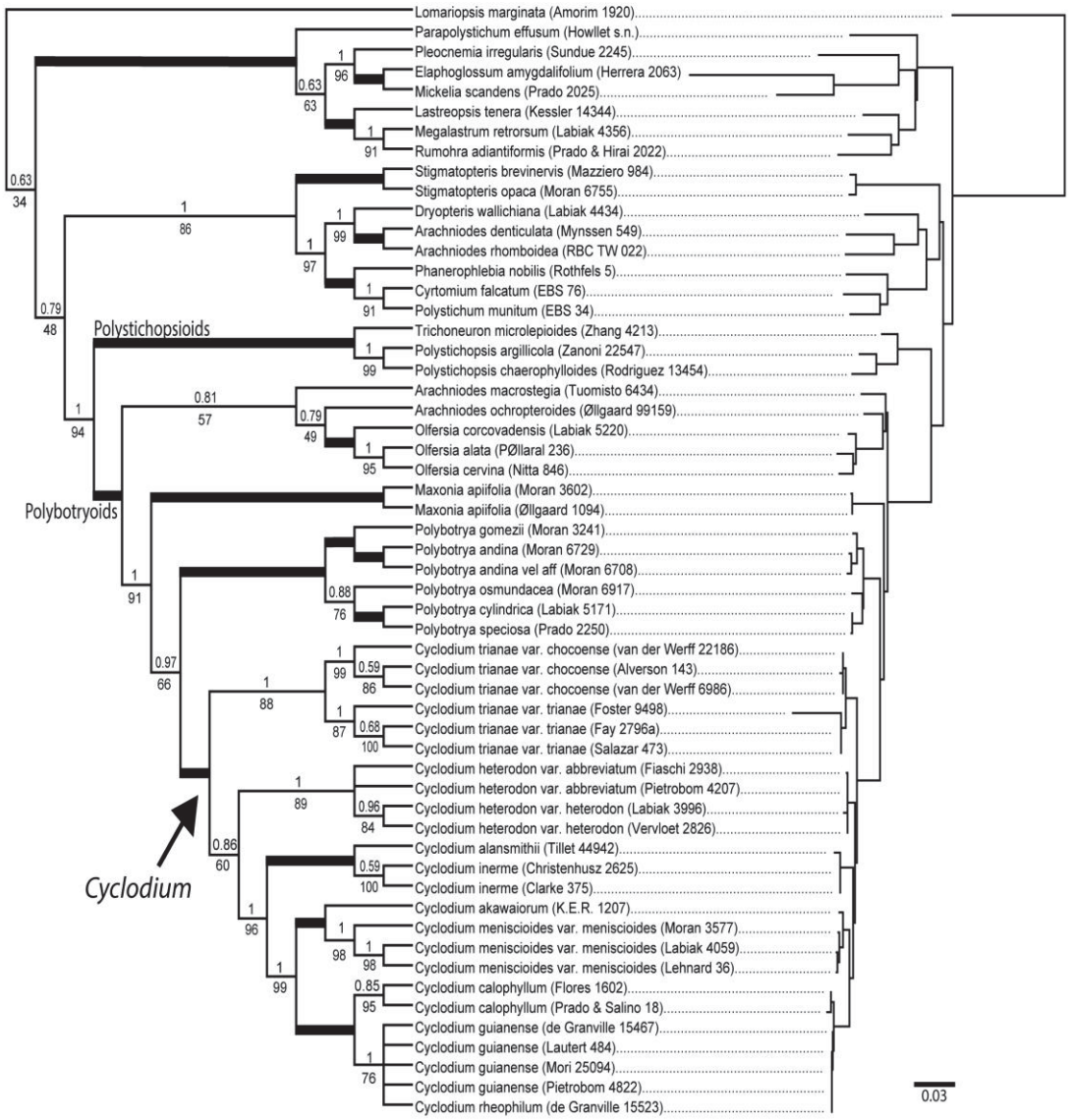


Fig. 3. Maximum Parsimony optimizations of four characters for *Cyclodium* and outgroups.

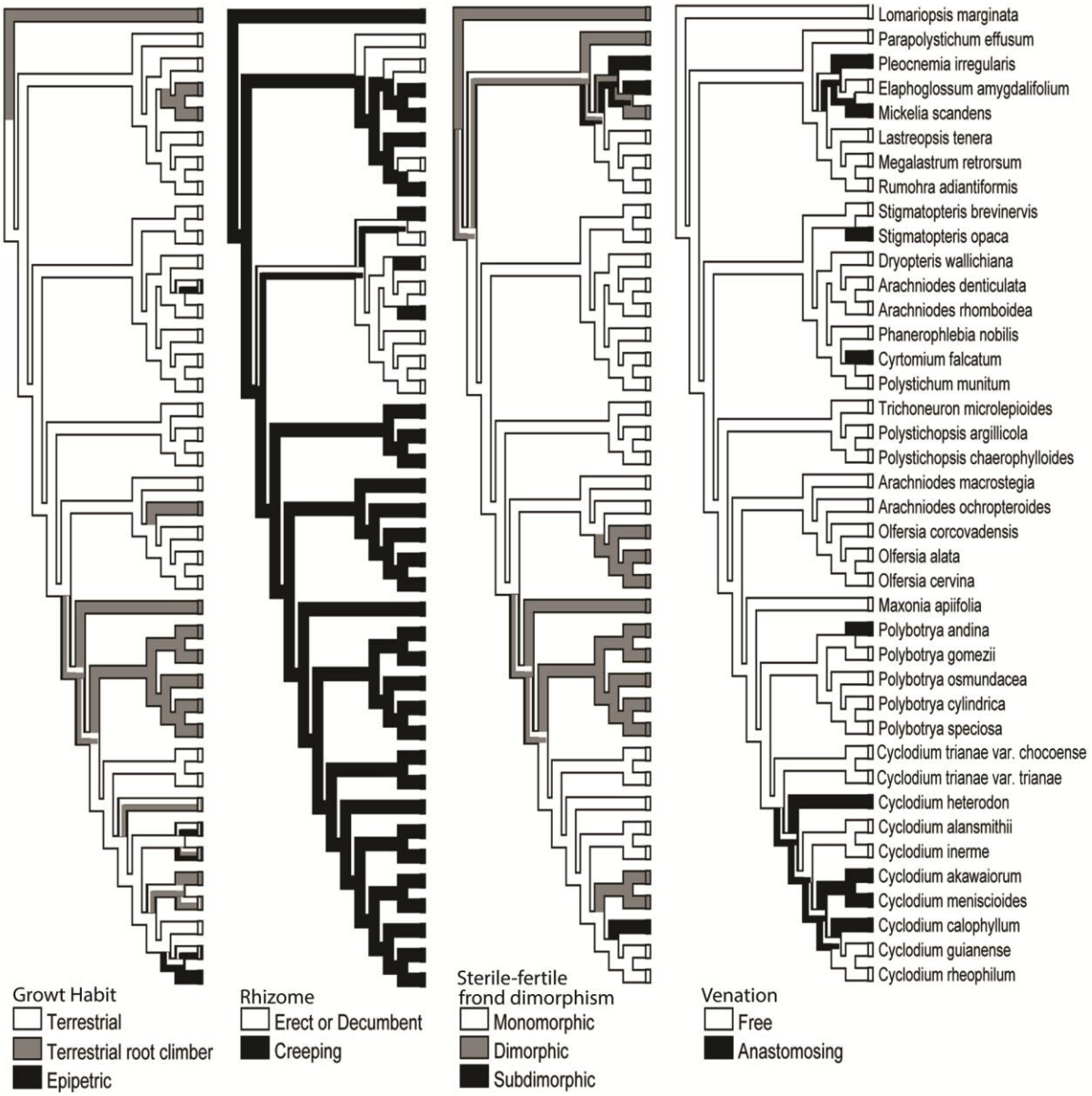


Fig. 4. Maximum Parsimony optimizations of three characters for *Cyclodium* and outgroups.

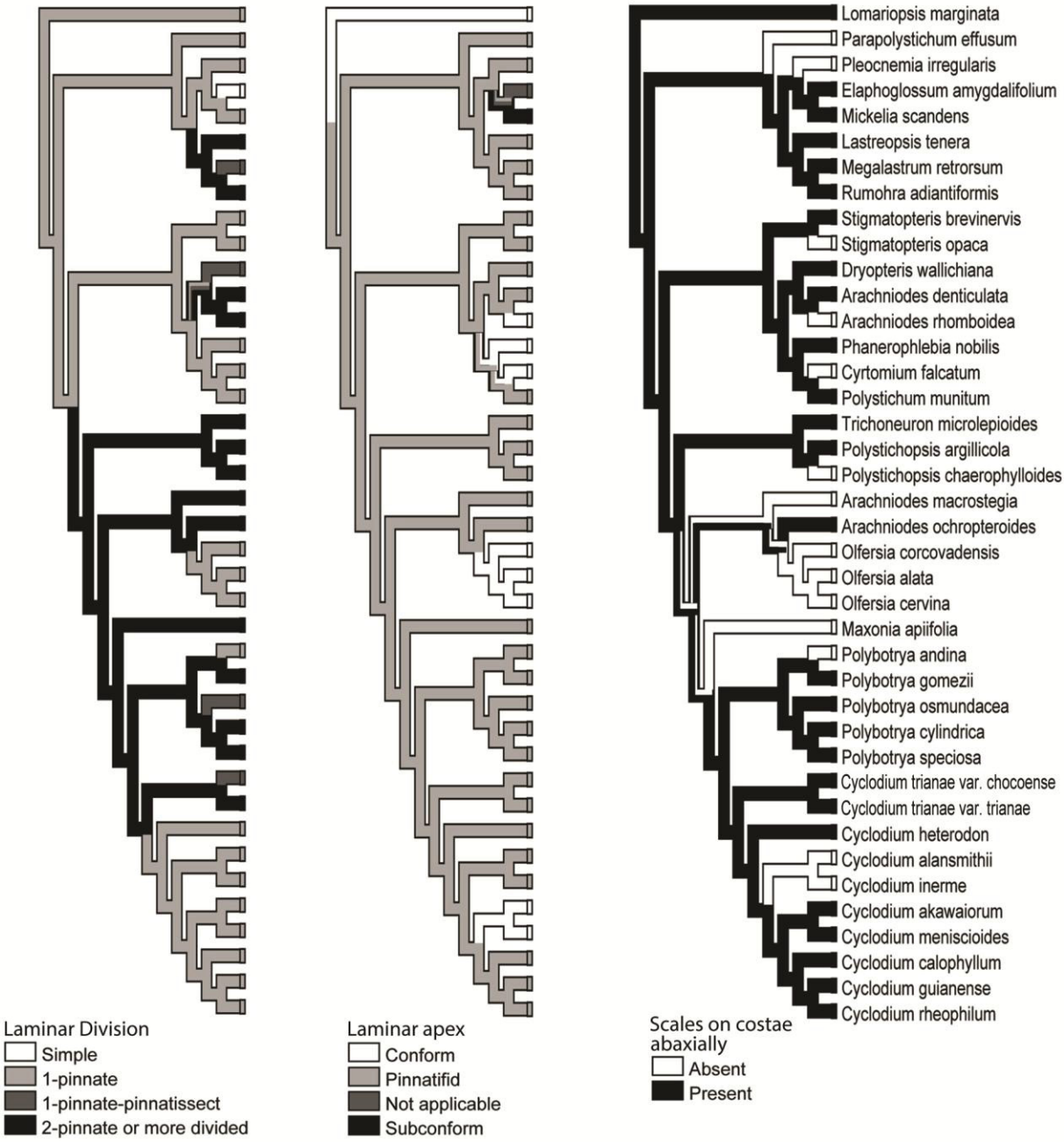


Fig. 5. Maximum Parsimony optimizations of three characters for *Cyclodium* and outgroups.

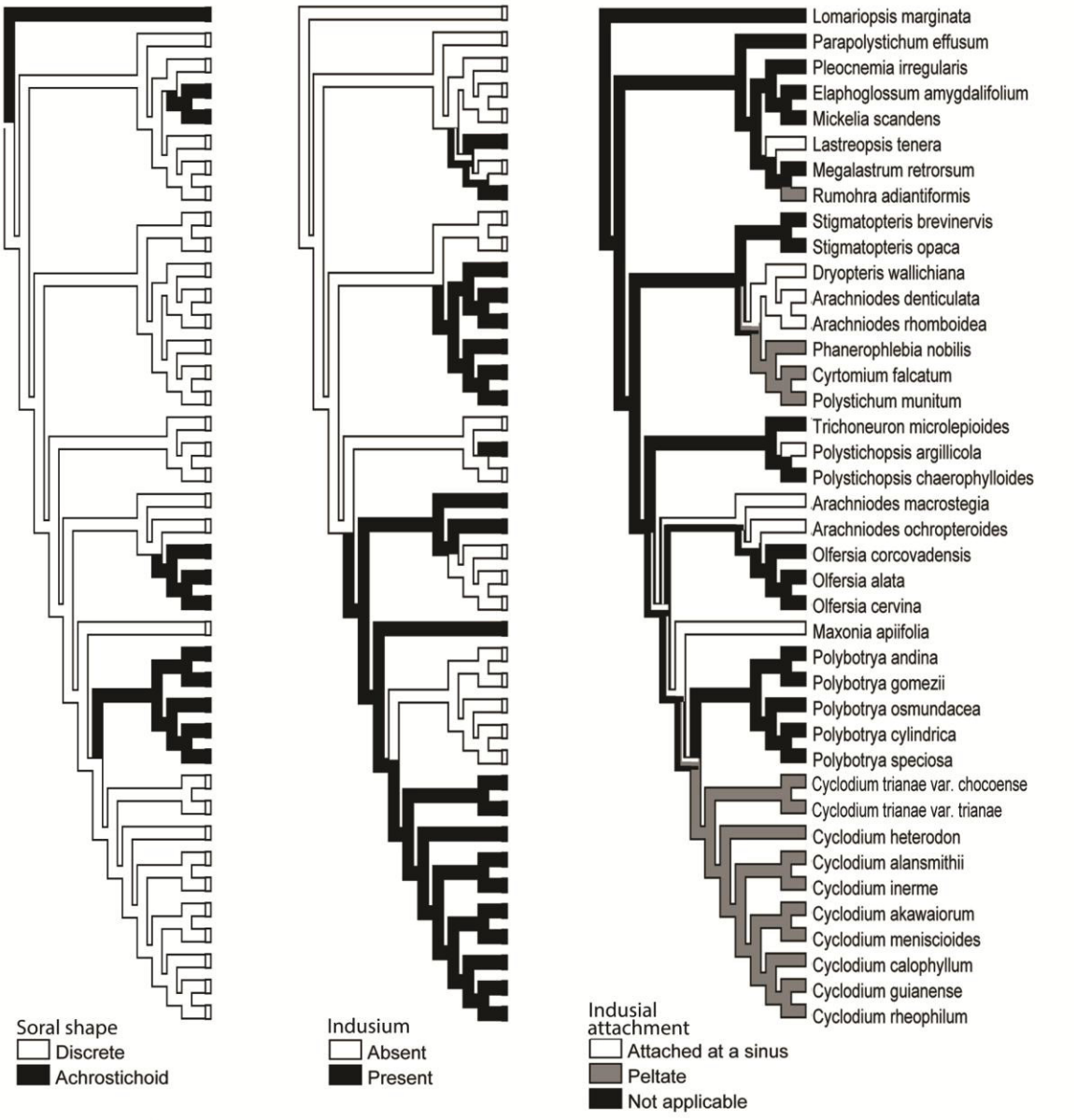
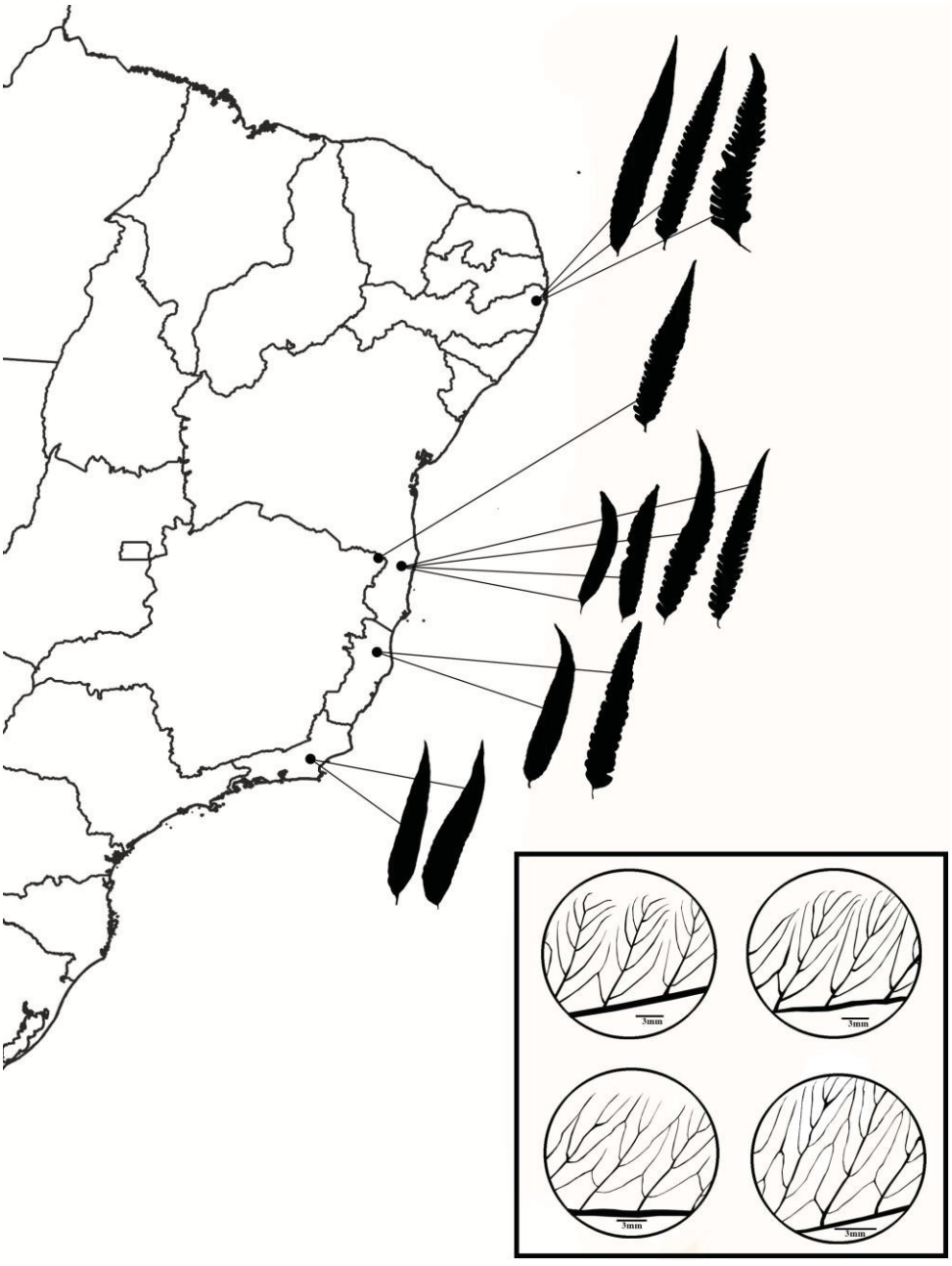


Fig. 6. Maximum Parsimony optimizations of three characters for *Cyclodium* and outgroups.

Fig. 7. Clinal variation of pinna lobing, and patterns of anastomosing venation (box) in *Cyclodium heterodon*. Images of pinna lobing from (top left to bottom right): *Gueiros* 239 (UFP), *Pietrobom* 4207 (UFP), *Pietrobom* 5090 (UFP), *Matos* 905 (UPCB), *Duarte* 6756 (UPCB), *Labiak* 3697 (UPCB), *Matos* 228 (UPCB), *Matos* 1095 (UPCB), *Labiak* 3996 (UPCB), *Duarte* 3610 (UPCB), *Brade* 14341 (UPCB), *Duarte* 154 (RB). Images of venation patterns from (top left to bottom right): *Duarte* 3610 (UPCB), *Gueiros* 239 (UFP), *Brade* 14341 (UPCB), *Duarte* 154 (RB).



Appendices

Appendix I. Voucher information and GenBank accessions for DNA sequences of *rbcL* gene, and *rps4-trnS, trnG-trnR, psbA-trnH,* and *trnP-petG* intergenic spacers of *Cyclodium* and outgroup.

Species	Voucher	Locality	*rbcl*	*rps4-trnS*	*trnG-trnR*	*psbA-trnH*	*trnP-petG*
Arachniodes denticulata (Sw.) Ching	Mynssen 549 (NY)	Brazil	KJ464419	KJ464663	KJ464510	X	X
Arachniodes macrostegia (Hook.) R.M.Tryon & D.S.Conant	Tuomisto 6434 (NY)	Peru	—	KT273003	KT273085	X	X
Arachniodes ochropteroides (Baker) Lellinger	Øllgaard 99159 (QCA)	Ecuador	KT272935	KT273009	KT273091	X	X
Arachniodes rhomboidea (Wall. ex Mett.) Ching	Cranfill TW 022 (UC)	—	JN189532	JN189206	JN188996	JN189424	JN189318
Cyclodium akawaiorum A.R.Sm.	K.E.R. 1207 (UC)	Guyana	—	X	—	X	X
Cyclodium alansmithii Bohn & Labiak	Tillet 44942 (NY)	Guyana	—	—	—	X	X
Cyclodium calophyllum (C.V.Morton) A.R.Sm.	Flores 1602 (NY)	Peru	—	X	—	X	X
Cyclodium calophyllum (C.V.Morton) A.R.Sm.	Prado & Salino 18 (UC)	Brazil	KT272936	—	KT273092	X	X
Cyclodium chocoense (A.R.Sm.) Bohn & Labiak	Alverson 143 (NY)	Colombia	—	X	—	X	—
Cyclodium chocoense (A.R.Sm.) Bohn & Labiak	van der Werff 6986 (UC)	Panama	—	X	—	X	—
Cyclodium chocoense (A.R.Sm.) Bohn & Labiak	van der Werff 22186 (MO)	Panama	X	X	X	X	X
Cyclodium guianense (Klotzsch) A.R.Sm.	de Granville 15467 (CAY)	French Guiana	—	X	—	X	X
Cyclodium guianense (Klotzsch) A.R.Sm.	Lautert 484 (MBM)	Brazil	—	X	—	X	X

Cyclodium guianense (Klotzsch) A.R.Sm.	Mori 25094 (NY)	French Guiana	KT272937	KT273010	KT273093	X	X
Cyclodium guianense (Klotzsch) A.R.Sm.	Pietrobom 4822 (NY)	Brazil	X	X	X	X	X
Cyclodium heterodon (Schrad.) T.Moore	Fiaschi 2938 (UPCB)	Brazil	X	X	X	X	X
Cyclodium heterodon (Schrad.) T.Moore	Labiak 3996 (UPCB)	Brazil	KJ464425	KJ464666	KJ464513	X	X
Cyclodium heterodon (Schrad.) T.Moore	Pietrobom 4207 (NY)	Brazil	—	X	—	X	X
Cyclodium heterodon (Schrad.) T.Moore	Vervloet 2826 (UPCB)	Brazil	X	X	X	X	X
Cyclodium inerme (Fée) A.R.Sm.	Christenhusz 2625 (NY)	Suriname	KT272938	KT273011	KT273094	X	X
Cyclodium inerme (Fée) A.R.Sm.	Clarke 375 (NY)	Guyana	X	X	—	X	X
Cyclodium meniscioides (Willd.) C.Presl	Labiak 4059 (UPCB)	Brazil	KT272939	KT273012	KT273095	X	—
Cyclodium meniscioides (Willd.) C.Presl	Lehnard 36 (UPCB)	Brazil	X	X	X	X	—
Cyclodium meniscioides (Willd.) C.Presl	Moran 3577 (QCA)	Ecuador	X	X	—	X	—
Cyclodium rheophilum A.R.Sm.	de Granville 15523 (NY)	French Guiana	KJ464426	KJ464667	KJ464514	X	X
Cyclodium trianae (Mett.) A.R.Sm.	Fay 2796a (UC)	Ecuador	X	X	X	X	X
Cyclodium trianae (Mett.) A.R.Sm.	Foster 9498 (NY)	Peru	—	—	—	X	—
Cyclodium trianae (Mett.) A.R.Sm.	Salazar 473 (QCA)	Ecuador	KU521865	KU521898	KU521935	X	X
Cyrtomium falcatum (L.f.) C.Presl	EBS 76 (WIS)	—	JN189561	JN189235	JN189022	X	X
Dryopteris wallichiana (Spreng.) Hyl.	Labiak 4434 (UPCB)	Brazil	KJ464428	KJ464669	KJ464516	X	X
Elaphoglossum amygdalifolium (Mett.) Christ	Herrera 2063 (NY)	Costa Rica	—	AY536173	—	—	—
Elaphoglossum amygdalifolium (Mett.) Christ	Moran 6952 (NY)	—	EF463184	—	—	—	—
Lastreopsis tenera (R.Br.) Tindale	Kessler 14344 (VT)	Australia	KJ464468	KJ464718	KJ464557	—	—
Lomariopsis marginata (Schrad.) Kuhn	Amorim 1920 (NY)	Brazil	AY818677	AY540049	—	—	—

Maxonia apiifolia (Sw.) C.Chr.	Moran 3602 (NY)	Ecuador	KT272941	KT273014	KT273097	X	X
Maxonia apiifolia (Sw.) C.Chr.	Øllgaard 1094 (QCA)	Ecuador	KT272942	KT273015	KT273098	X	X
Megalastrum retrorsum R.C.Moran, J.Prado & Labiak	Labiak 4356 (UPCB)	Brazil	KJ464485	KJ464736	KJ464572	—	—
Mickelia scandens (Raddi) R.C.Moran, Labiak & Sundue	Prado 2025 (SP)	Brazil	KJ464488	—	—	—	—
Olfersia alata C.Sánchez & Caluff	Pøllaral 236 (NY)	Cuba	X	KT273018	—	X	X
Olfersia cervina Kunze	Labiak 5220 (UPCB)	Brazil	KJ464493	KJ464741	KJ464577	X	X
Olfersia cervina Kunze	Nitta 846 (NY)	Costa Rica	KT272944	KT273020	—	X	X
Parapolystichum effusum (Sw.) Ching	Howllet s.n. (VT)	—	AF537230	X	X	—	—
Phanerophlebia nobilis (Schltdl. & Cham.) C.Presl	Rothfels 5 (DUKE)	—	JN189569	JN189242	JN189030	JN189459	—
Pleocnemia irregularis (C.Presl) Holttum	Sundue 2245 (VT)	Philippines	KJ464494	KJ464742	KJ464578	—	—
Polybotrya andina C.Chr.	Moran 6729 (NY)	Ecuador	KJ464498	KJ464746	KJ464582	X	X
Polybotrya andina vel aff	Moran 6708 (NY)	Ecuador	KT272952	KT273028	KT273107	X	X
Polybotrya cylindrica Kaulf.	Labiak 5171 (UPCB)	Brazil	KT272961	KT273038	KT273116	X	X
Polybotrya gomezii R.C.Moran	Moran 3241 (NY)	Costa Rica	KT272966	KT273043	KT273121	X	X
Polybotrya osmundacea Humb. & Bonpl. ex Willd.	Moran 6917 (NY)	Ecuador	KT272976	KT273057	KT273131	X	X
Polybotrya speciosa Schott	Prado 2250 (SP)	Brazil	KT272989	KT273072	KT273144	X	X
Polystichopsis argillicola Proctor	Zanoni 22547 (NY)	Dominican	X	X	—	X	X

		Republic					
Polystichopsis chaerophylloides (Poir.) C.V.Morton	Rodriguez 13454 (NY)	Puerto Rico	KT272996	KT273079	KT273150	—	—
Polystichum munitum (Kaulf.) C.Presl	EBS 34 (WIS)	—	JN189508	JN189182	JN188971	JN189399	JN189293
Rumohra adiantiformis (G.Forst.) Ching	Prado & Hirai 2022 (NY)	Brazil	KJ464502	KJ464749	KJ464586	MF157935	—
Stigmatopteris brevinervis (Fée) R.C.Moran	Mazziero 984 (UPCB)	Brazil	KU521867	KU521900	KU521937	—	—
Stigmatopteris opaca (Baker) C.Chr.	Moran 6755 (NY)	Ecuador	KU521892	KU521925	KU521960	—	—
Trichoneuron microlepioides Ching	Zhang 4213 (XC)	Vietnam	KT831882	—	—	—	—

† "X" indicates newly obtained sequences that were not yet submitted to GenBank. "—" indicates missing data.

CAPÍTULO 2 - Taxonomic novelties in *Cyclodium* (Dryopteridaceae): a new species, a new status, and a key to the species with free veins

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Taxonomic novelties in *Cyclodium* (Dryopteridaceae)

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Background – *Cyclodium* is a neotropical fern genus comprising about ten species. Most species are found in northern South America, and the foothills of the Guiana Shield is an important region for species diversification. Our phylogenetic and taxonomic studies of the genus demonstrated the need to describe a new species and to recognize a variety at species level.

Methods – This study is based on herbarium specimens from CAY, HUA, INPA, MBM, NY, P, RB, UC, UFP, UPCB, and US. Morphological characters were analyzed using standard procedures. The indument and spores of the new species were studied using a scanning electron microscope. Species delimitation is proposed based on our preliminary phylogenetic studies, as well as on morphology and geographical distribution.

Key results – *Cyclodium alansmithii* Bohn & Labiak is recognized as a new species, described, and illustrated. The most similar species is *Cyclodium inerme* (Fée) A.R.Sm., from which it differs by ovate-lanceolate and bicolored scales, reduced fronds, truncate pinna bases, and non-ciliate indusia. *Cyclodium alansmithii* is currently assessed as Endangered (EN) using IUCN criteria, but more fieldwork and herbarium studies are necessary. *Cyclodium trianae* (Mett.) A.R.Sm. var. *chocoense* A.R.Sm. is here elevated to species rank. A key to species of *Cyclodium* with free veins is provided.

Key words – Amazon, Biodiversity, Ferns, Guayana Shield, Polybotryoids, Taxonomy.

INTRODUCTION

Cyclodium C.Presl (Dryopteridaceae) is entirely neotropical, with about ten species distributed from Trinidad and Panama to northeastern Argentina and eastern Brazil, usually below 1500 m of altitude (Smith 1986). The greatest diversity is found in the Guianas, where six species and many putative hybrids occur (Cremers et al. 1993). The most recent comprehensive study of *Cyclodium* is that of Smith (1986), and since then the genus has appeared in numerous regional floras and checklists (e.g., Tryon & Stolze 1991; Cremers et al. 1993; Smith & Moran 1995; Smith et al. 1995; Mori et al. 1997; Santiago & Barros 2003; Garcia & Salino 2008; Almeida & Salino 2015; Kessler et al. 2018). Additionally, two intergeneric hybrids involving a cross of *Cyclodium meniscioides* (Willd.) C.Presl with different species of *Polybotrya* Humb. & Bonpl. ex Willd. have been recently described from Brazil (Engels & Canestraro 2017; Schwartsburd et al. 2017), suggesting that hybridization may have played an important role in the evolution and diversification of *Cyclodium*.

The genus is characterized by short- to long-creeping rhizomes, 1–2-pinnate fronds (rarely more divided), chartaceous to subcoriaceous laminae, and peltate indusia. Most of its species are terrestrial, but there are records of hemiepiphytic, epiphytic, epipetric, and rheophytic plants (Smith 1986). Some of these characters are also present in other dryopteroid genera, such as *Maxonia* C.Chr.*, Olfersia* Raddi*, Polybotrya,* and *Stigmatopteris* C.Chr. Some earlier authors (e.g., Christensen 1913, 1920; Tryon & Tryon 1982; Smith 1986; Moran 1987, 1991a) have used these similarities to suggest affinities between these genera on the basis of morphology. More recently, phylogenetic studies based on plastid DNA recovered *Cyclodium* as monophyletic and sister to *Polybotrya*, forming a clade with other dryopteridoid ferns that have creeping rhizomes and (often) fertile-sterile leaf dimorphism (Moran & Labiak 2015; PPG I 2016).

During our phylogenetic (ten taxa of the genus, five cloroplastidial markers) and taxonomic studies on *Cyclodium* (Bohn et al., in prep.), we found some taxonomic novelties that we present herein. They include a new species, *Cyclodium alansmithii,* and a new status for *C. trianae* (Mett.) A.R.Sm var. *chocoense*. Because both species have free veins, we also provide a dichotomous key to all free-veined species of *Cyclodium*.

MATERIALS AND METHODS

Herbarium specimens were obtained as loans from CAY, HUA, INPA, MBM, NY, P, RB,

UC, UFP, UPCB, and US (Thiers 2018). Additional images of type specimens were accessed on JSTOR (https://plants.jstor.org/). For morphological descriptions, the largest fertile and sterile pinnae were measured. Measurements of hairs and scales were made using a trinocular stereo microscope (AmScope SM-3TX) equipped with a 54-bulb LED illumination and MU500 5MP digital camera. SEM images of the spores, scales, and hairs were obtained using a JEOL JSM-6360LV scanning electron microscope at the Electron Microscopy Center of Universidade Federal do Paraná. The material was transferred with dissecting needles from herbarium specimens to aluminum stubs coated with asphalt adhesive. The stubs were sputter-coated with gold for two minutes. Hairs, scales, proscales, and indusia were imaged digitally with an optical microscope LEICA MZ16 equipped with a camera (LEICA DFC 500) at the Department of Zoology, Universidade Federal do Paraná. Information about the geographical distribution was obtained from herbarium labels, and the maps were made using QGIS 3.2.0 software (Quantum GIS Development Team 2013). When not provided, geographical coordinates were estimated, and are presented within brackets. The layers included a raster file (1: 10,000,000), from Natural Earth (www.naturalearthdata.com), and shape files (political units and rivers), obtained from the Organization for Flora Neotropica (www.nybgpress.org). The conservation status of the new species was obtained using the GeoCAT tool from Kew (http://geocat.kew.org/).

TAXONOMIC TREATMENT

Cyclodium alansmithii Bohn & Labiak, **sp. nov.**

This species is similar to *Cyclodium inerme* (Fée) A.R.Sm. by having 1-pinnate laminae, pinnae with crenate margins, and free veins, with the basal veinlets arising from costules and ending below or right above the sinuses. It differs from *C. inerme* by its smaller fronds, ovate-lanceolate and bicolorous rhizome scales, pinnae with truncate bases, and indusia with non-ciliate margins. It is also similar to *Cyclodium guianense* (Klotzsch) A.R.Sm., from which it differs by the absence of conspicuous costal scales. – Type: Guyana, Upper Mazaruni River Basin, Mt. Ayanganna, [05°22’03.4”N, 59°56’51.8”W], alt. 800 m, 27 Jul. 1960, *Tillett* 44942 (holo-: NY [2859537], iso-: US [719099]).

Plants terrestrial or epipetric. Rhizomes short-creeping, 0.3–0.5 (–1) cm diam., with ca. 6–10 fronds per 3 cm, scaly at apex; scales basifixed, ovate-lanceolate, 3–5 × 0.5–1 mm,

bicolorous, brown, with thinner, lighter margins, these entire to slightly erose. Fronds monomorphic to subdimorphic, lanceolate to elliptic; sterile fronds (31–) 37.5–50 (–63) × 8.5–10.5 (–17) cm, fertile fronds (29.5–) 37–64.5 (–80) × (8–) 10–14 cm; petioles stramineous to tan, with scattered scales, rarely with septate, linear, brown proscales, 11–18 (–36) cm long in sterile fronds, 16.5–36.5 (–48) cm long in fertile fronds, 1.5–3 mm diam.; petiole scales basifixed and with a sinus or peltate, ovate-lanceolate, appressed, 1.5–5 × 0.5–3 mm, bicolorous, brown, with thinner, lighter margins, these entire to slightly fimbriate; laminae 1-pinnate pinnatifid, with (11–) 15–25 pairs of lateral pinnae, sometimes overlapping towards apex and gradually reduced to a pinnatifid apex; (18–) 23.5–32.5 × 8.5–10.5 (–17) cm in sterile fronds, (13–) 17.5–34 × (6.5–) 7.5–12.5 cm in fertile fronds; rachises stramineous to tan, with an elevated center and two shallow lateral grooves abaxially and a central groove adaxially, the grooves with bacilliform, translucid, yellowish hairs ca. 0.1 mm long, abaxially glabrous or with septate, linear, brown to dark brown, scattered proscales, rarely with brown scales, ca. 1.5–2 cm long; pinna stalks 1.5–3 (–4) mm long, with bacilliform, translucid, yellowish, glandular hairs and proscales similar to those of the rachises; pinnae linear to elliptic, bases truncate, sometimes subauriculate acroscopically, apices acute to round, margins undulate or crenate to pinnatifid margins, more dissected in fertile fronds, sterile basal pinnae (3.8–) 4.5–8 × 1.3–2 cm, fertile basal pinnae (2.5–) 3.5–6 (–8) × (0.7–) 1–1.4 (–2) cm, sterile medial pinnae 3.8–5.3 (–7) × 1.1–1.6 cm, fertile medial pinnae (2.6–) 3–6 × 0.7–1.6 cm; costae abaxially with linear, septate, brown to dark brown proscales; laminar tissue glabrescent, with septate, light brown proscales; veins free, conspicuous, 3–4-furcate, the basal veins ending below or immediately above the sinuses, rarely reaching the margins; sori discrete, impressed, medial on veins, forming 2 or 3 (–4) rows between costae and margins, biseriate between two main lateral veins; indusia peltate, sometimes with stalks slightly dislocated from center, circular, ca. 0.5–1 mm diam, concolorous, stramineous, with entire to erose margins; spores monolete, 50–55 μm diam., perines broadly folded and densely echinulate, the folds low and continuous. Figs 1–3.

Distribution – Guyana (Cuyuni-Mazaruni and Potaro-Siparuni Regions) and Venezuela (Bolívar). Figure 4.

Other collections examined – **Guyana**: Cuyuni-Mazaruni Region, Aurora, creek ± 1 km WSW of camp, 06°47'N, 59°44'W, alt. 70–75 m, 12 Oct. 1989, *Gillespie* 2288 (INPA); Cuyuni-Mazaruni Region, at headwaters of Kangu River, W branch, ± 4 km NW of E peak of

Mt. Ayanganna, first talus slope of plateau, 05°25'N, 60°00'W, alt. 700 m, 5 Mar. 1987, *Pipoly* 11045 (US); Cuyuni-Mazaruni Region, below 1st escarpment (of four) of Kamakusa Mt., 0-1.5 mi SW of Micrandra (4th) Camp, 05°51'08"N, 60°11'17"W, alt. 840 m, 29 May 2012, *Wurdack* 5749 (CAY); Cuyuni-Mazaruni Region, Kako river, Chinakuruk Mountain, cliff foot of mountain, [05°31'47"N, 60°42'39"W], alt. 1226 m, 21 May 2009, *Redden* 6709 (NY); Cuyuni-Mazaruni Region, Pakaraima Mtns, Kumarau Falls on Kurupung R, 0.2–1.0 km N along river gorge edge, 06°06'N, 60°21'W, alt. 300–340 m, 01 Aug. 1992, *Hoffmann* 2248 (CAY); Cuyuni-Mazaruni Region, Pakaraima Mountains, Kurupung-Membaru trail, 2.75 km from Kumarau Falls, 06°05'N, 60°23'W, alt. 650 m, 22 Jul. 1992, *Hoffman* 2109 (CAY); Potaro-Siparuni Region, Kaieteur National Park, W bank Potaro River, 0.5 km from falls in gorge, 05°11'N, 59°28'W, alt. 170 m, 12 Jul. 1993, *Henkel* 2174 (CAY); Potaro-Siparuni Region, Marina Falls, 05°22'43"N, 59°28'93"W, alt. 449 m, 28 Mar. 2011, *Zartman* 9359 (INPA); Potaro-Siparuni Region, Mt. Ayanganna, east face, camp at base of first of four escarpments, 05°22'22"N, 59°57'34"W, 16 Jun. 2001, *Clarke* 9199 (NY); Potaro-Siparuni Region, Pakaraima Mts., Mt. Korak, Mazaruni R., 05°59'N, 60°37'W, alt. 600 m, 14 Nov. 1979, *Maas* 4436 (NY); Potaro-Siparuni Region, Pakaraima Mts, Mt. Wokomung, Suruwabaru Creek, 2–3 km upstream from its juncture with Yuarka R, 05°03'N, 59°53'W, alt. 675–750 m, 10 Feb. 1993, *Henkel* 1222 (CAY, NY); Potaro-Siparuni Region, Pakaraima mts., Mt. Wokomung; Suruwabaru Creek, 12 km from juncture with Yuarba River, 05°02'N, 59°54'W, alt. 675–750 m, 57 Nov. 1993, *Henkel* 4106 (NY); Potaro-Siparuni Region, upper Kuribrong River, 05°34'20"N, 59°54'22"W, 20 Mar. 2011, *Zartman* 9172 (INPA); Potaro-Siparuni Region, Potaro River gorge, [05°10'0.72"N, 59°28'0.71"W], 17 May 1944, *Maguire* 23525 (NY). **Venezuela:** Bolívar, Chimantá Massif, southwestern-facing forested slopes of Chimantá-tepuí (Torono-tepuí), between Base Camp and steep slopes above valley of Río Tirica, [05°18'43"N, 62°07'23"W], alt. 1000–1400 m, 15 May 1953, *Steyermark* 75376 (US).

Habitat and ecology – This new species is often associated to creeks and hillsides, growing on sandstone soils between 170–1400 m in elevation. Most specimens are terrestrial, but some are epipetric. One specimen (*Steyermark* 75376, US00798729), is unusual because it occurs at lower elevations, between 70–75 m, in "terra firme" forest. The region where *C. alansmithii* occurs is part of the Guiana Shield, the remainder of an ancient craton older than the Gondwana dissociation, that extends from southwestern Venezuela, Guyana, Suriname, French Guiana, to northern Brazil and southeastern Colombia (Funk & Berry 2005). The most comprehensive work for the Guiana Shield region is from Berry et al. (1995), which analyzed

the Venezuelan Guayana, and found high diversity and endemicity of fauna and flora. This region is known to have diverse geological formations, such as tepuis and inselbergs, with several habitats, as tropical savannas, lowland and montane forests, as well as shrub, and herbaceous formations (Berry et al. 1995). Most regions from the Guiana Shield are still untouched (ca. 60–70%), and programmes to encourage conservation are recent. The most comprehensive of them is The Biological Diversity of the Guiana Shield (BDG), which since 1983 is conducted by the Smithsonian Institution's National Museum of Natural History.

Etymology – The specific epithet honours Alan R. Smith (1943–), American pteridologist and author of a detailed taxonomic revision of *Cyclodium* (Smith 1986).

Conservation assessment – According to IUCN categories and criteria (IUCN 2001), *Cyclodium alansmithii* is considered least concern (LC). Its extent of occurrence (EOO) is 29,142.139 km², which exceeds the threshold of 20.000 km² for the vulnerable category under criterion B1. The area of occupancy (AOO) was estimated at 60.000 km² (lower than the threshold of 500 km² of B2 criteria for endangered category) and is endangered (EN) under criterion B2a, bii.

Notes – *Cyclodium alansmithii* can be recognized by its ovate-lanceolate, bicolored rhizome and petiole scales, reduced fronds (generally ca. 30–65 × 8–14 cm), 1-pinnate laminae, pinnae with truncate bases and crenate margins, and free venation. From the six species that occur in Guyana (Cremers et al 1993), it mostly resembles *C. inerme* by its free veins with the basal veinlets arising from costules and ending below or right above sinus, pinnae with crenate margins, costal grooves virtually glabrous adaxially, and lack of conspicuous scales abaxially. Also similar is *C. guianense*. The main differences regarding *C. inerme* and *C. guianense* are given in the diagnosis above. Two other species that also have bicolorous rhizome scales are *C. meniscioides*, and *C. akawaiorum* A.R.Sm. They both differ from *C. alansmithii* by having anastomosing veins. Another species from French Guiana, *Cyclodium rheophilum* A.R.Sm., also resembles *C. alansmithii*, but differs by having concolorous rhizome scales, narrower pinnae (1–2 cm vs. 0.3–0.6 cm), conspicuous costal scales, and reniform indusia.

Cyclodium chocoense (A.R.Sm.) Bohn & Labiak, **stat. nov.**
Cyclodium trianae (Mett.) A.R.Sm. var. *chocoense* A.R.Sm. (Smith 1986: 93). – Type: Colombia, Chocó, Corcovado region, upper Río San Juan, ridge along Yeracüí Valley, alt.

200–275 m, 24–25 Apr. 1939, *Killip* 35287 (holo-: US [01050249], iso-: COL n.v.)

Distribution – *Cyclodium chocoense* is distributed from Panama through western Colombia and Ecuador (first record in Ecuador), whereas *C. trianae* occurs from Panama to Peru. Even though they co-occur in Panama and north of Colombia, *C. trianae* is found only on the eastern side of the Andes, whereas *C. chocoense* occurs only on the western side. Figure 5.

Other collections examined – **Panama:** Panama, Cerro Azul, cabecera del río San Cristobal, [9°13'52"N, 79°21'02"W], alt. 900 m, 28 Dec. 1986, *Valdespino* 289 (UC); Cerro Jefé, [9°13'58"N, 79°21'01"W], 16 Feb. 1985, *van der Werff* 6986 (UC); San Blas, Kuna Yala, hills of Sperdi, near Puerto Obaldía, San Blas coast, [8°39'57"N, 77°25'05"W], alt. 20–200 m, Sep. 1911, *Pittier* 4415 (US). **Colombia:** Antioquia, Anorí, vereda Puntiadero o la Concha abajo, quebradas El Salto y El Claro, sector la Concha abajo, 7°17'01.2"N, 75°05'17.1"W, alt. 720 m, 16 Jan. 2004, *Rodríguez* 4461 (COL web); Mutatá, Finca El Dárien, [7°14'47"N, 76°26'00"W], alt. 200 m, 18 May 1976, *Atehortúa* 216 (HUA web); Corregimiento Longaní, margem derecha del Rio Longaní, 2 km al norte de Mutatá, [7°14'21"N, 76°26'03"W], alt. 80–100 m, 19 Nov. 1987, *Alberláez* 248 (HUA web); San Luis, vía Medellín-Bogotá, quebrada La Tebaída, 6°8'N, 75°10'W, alt. 1010–1060 m, 22 Jun. 1987, *Callejas* 4002 (HUA web, NY); Vic. Planta Providencia, 26 km S & 23 km W (air) of Zaragoza, in valley of rio Anorí between dos Bocas & Anorí, 7°13'N, 75°03'W, alt. 400–700 m, 2 Mar. 1977, *White* 140 (HUA web); Vic. Planta Providencia, 26 km S & 23 km W (air) of Zaragoza, in valley of rio Anorí between dos Bocas and Anorí, 7°13'N, 75°03'W, alt. 400–700 m, 13 Jun. 1976, *Sheperd* 432 (HUA web); Vic. Planta Providencia, 28 km SW of Zaragoza, valley of Río Anorí in aread surronding the confluence of quebrada La Tirana and Río Anorí, approx. 3 km upriver from Plant Providencia, 7°18'N, 75°04'W, alt. 400–700 m, 4 Mar. 1977, *Alverson* 143 (HUA web, NY); Bajo Calima, Buenaventura, Secretaria de Agricultura, [3°59'47"N, 76°58'35"W], alt. 80 m, 31 Mar. 1984, *de Escobar* 4000 (HUA web); Bajo Calima, Buenaventura, Secretaria de Agricultura, [3°59'47"N, 76°58'35"W], alt. 70 m, 1 Apr. 1984, *de Escobar* 4025 (HUA web); Caldas, Sanamá, El Carmén, 05°31'36"N, 75°02'26"W, 7 May 1992, *César* 6973 (HUA web); Cauca, Timbiquí, east side of Gorgona Island, dense forest along stream, [2°49'58"N, 77°42'24"W], alt. 50–100 m, 11 Feb. 1939, *Killip* 33172 (COL web); Chocó, Bahía Solano, dense forest along Quebrada Jella, near ciudad Mutis, [6°12'34"N, 77°18'08"W], alt. 0–75 m, 21–23 Feb. 1939, *Killip* 33622 (COL web); Chocó, Bahía Solano, km 11 between El Valle and ciudad Mutis, [6°13'47"N, 77°22'54"W], alt. 50 m, 15 Feb. 1986,

Wood 5296 (COL web); Chocó, Bahía Solano, low hills behind the beach 1–1.5 km NW of El Valle, N of the lagoon, [6°07'48"N, 77°26'26"W], alt. 25–75 m, 13 Feb. 1971, *Lellinger* 343 (COL web); Chocó, Bahía Solano, near Punta San Francisco Solano, ca. 10 km NE of Puerto Mutis, [6°14'40"N, 77°23'15"W], alt. 10–100 m, 27 Jan. 1971, *Lellinger* 82 (HUA web); Chocó, Bahía Solano, NW side of Alto del Buey, trail along ridge from the confluence of the forks of the rio Mutatá above Río Dos Bocas toward the top of Alto del Buey, [6°08'08"N, 77°19'38"W], alt. 950–1450 m, 8–10 Feb. 1971, *Lellinger* 211, 253 (COL web, HUA web); Chocó, Canton Del San Pablo, pan american Highway (under construction), ca. 10 km W of las Animas, [5°17'41"N, 76°41'01"W], alt. 100 m, 12 Jan. 1979, *Gentry* 24057 (COL web); Chocó, carretera Andagoya-Condoto, cerca de Andagoya, 5°06'N, 76°40'W, 14 Apr. 1979, *Forero* 5288 (COL web); Chocó, Istmina, dense forest near junction of Rio Condato and rio San Juan, [5°05'50"N, 76°41'47"W], alt. 100–150 m, 20 Apr. 1939, *Killip* 35084 (COL web); Chocó, Istmina, río Bicordó, arriba de Noanamá, orillas del rio, 4°42'N, 76°55'W, 6 Apr. 1979, *Forero* 4753 (COL web); Chocó, Istmina, rio El Salto (tributary of the Río Suruco), 9 km W of Andagoya, [5°05'32"N, 76°44'17"W], alt. 75–100 m, 23 Feb. 1971, *Lellinger* 478 (COL web); Chocó, Istmina, Río Fujiadó, afluente del Río San Juan, 4°36'N, 76°54'W, 7 Apr. 1979, *Forero* 4813 (COL web); Chocó, Litoral Del Bajo San Juan, Region del río Pichimá, comunidad indigena Waunana, 4°25'N, 77°17'W, 23 Nov. 1976, *Forero* 746 (COL web); Chocó, Nóvita, quebrada Máncamo, afluente del Rìo Tamaná, cerrito em la margen izquierda, 4°57'N, 76°38'W, 11 Apr. 1979, *Forero* 5051 (COL web); Chocó, Nuqui, corregimiento Termales, quebrada Piedra Piedra, [5°42'32"N, 77°15'55"W], alt. 0–25 m, 6 Sep. 1994, *Acevedo-Rodriguez* 6807 (HUA web); Chocó, carretera Quibdó-Tutunendo, 15 km de Quibdó, [5°43'39"N, 76°36'10"W], alt. 45 m, 6 Sep. 1976, *Forero* 2528 (COL web); Chocó, margem izquierda del río Munguidó, afluente del río Atrato, en pequeno cerro cerca de Altagracia, [5°42'38"N, 76°46'27"W], alt. 50 m, 4 May 1975, *Forero* 1535 (COL web); Chocó, río Serrano, afluente del río Atrato, 4-6 km arriba del Guayabal, [5°44'37"N, 76°38'37"W], alt. 50 m, 29 Apr. 1975, *Forero* 1342 (COL web, NY); Chocó, Tadó, Corcovada region, upper Río San Juan, ridge along Yeracüí Valley, [5°20'15"N, 76°15'05"W], alt. 200–275 m, 25–26 Apr. 1939, *Killip* 35287 (COL web); Chocó, Mojarras de Tadó, 8.5 km E of Istmina, [5°16'14"N, 76°33'04"W], alt. 150–250 m, 20 Feb. 1971, *Lellinger* 417 (COL web); Chocó, Unión Panamericana, quebrada Peña Negra, 8 km W of Quidbó-Istmina road on new Pan American Highway, [5°17'04"N, 76°39'33"W], alt. 90 m, 10 Jan. 1979, *Gentry* 23937 (COL web, HUA web); Nariño, Barbacoas, al W de El Diviso, [1°22'40"N, 78°13'59"W], alt. 350 m, 3 Jun. 1973, *Leist* 2158 (COL web); Nariño, carretera Barbacoas-

Junin, km 8, [1°32'58"N, 78°05'44"W], alt. 140 m, 18 Dec. 1972, *Hagemann* 1702 (COL web); Nariño, San Andres de Tumaco, km 80, [1°45'33"N, 78°47'07"W], alt. 300 m, 1 Nov. 1967, *Mora* 4222 (COL web); Valle del Cauca, Buenaventura, about 18 km east of Buenaventura, dense forest, [3°53'56"N, 76°58'58"W], alt. 50 m, 14 Feb. 1939, *Killip* 33246 (COL web); Valle del Cauca, Bajo Calima, [3°53'04"N, 77°00'39"W], 2 Apr. 1984, *de Escobar* 4061 (HUA web); Valle del Cauca, Bajo Calima, Concesión Pulpapel/Buenaventura, 3°55'N, 77°00'W, alt. 100 m, 20 Sep. 1984, *Monsalve* 433 (UC); Valle del Cauca, corregimiento San Cipriano, Reserva Natural de Escalerete, bajando de la casa blanca, [3°55'59"N, 77°10'00"W], alt. 100 m, 14 Apr. 1993, *Cruz* 4044 (COL web); Valle del Cauca, costa del Pacífico, río Cajambre, quebrada del Corosal, [3°30'47"N, 77°14'03"W], 17 May 1944, *Cuatrecasas* 17731 (UC); Valle del Cauca, dense forest near highway bridge over Río Dagua, about 20 km east of Buenaventura, [3°50'34"N, 76°47'26"W], alt. 40 m, 15 Feb. 1939, *Killip* 33320 (COL web); Valle del Cauca, hoya del río San Juan, alrededores de Palestina, 4°10'N, 77°10'W, alt. 5 m, 26 Mar. 1979, *Forero* 4035 (COL web); Valle del Cauca, quebrada Taparal, afluente del río San Juan, alrededores de la comunidad indigena Waunaná de Taparalito, 4°10'N, 77°10'W, alt. 5–10 m, 28 Mar. 1979, *Forero* 4269 (COL web); Valle del Cauca, quebrada La Sierpe, afluente del Río San Juan, 4°10'N, 77°10'W, alt. 5 m, 1 Apr. 1979, *Forero* 4449, 4450 (COL web); Valle del Cauca, Dagua, Agua Clara, along highway from Buenaventura to Cali, [3°44'50"N, 76°43'11"W], alt. 100 m, 6 Jun. 1944, *Killip* 38991 (US); Valle del Cauca, carretera Cali-Buenaventura, rio Danubio inferior, [3°43'38"N, 76°40'09"W], alt. 200 m, 15 Sep. 1967, *Hagemann* 424 (COL web). **Ecuador:** Esmeraldas, San Lorenzo, territorio Indígena Awá, Mataje village, 500 m west of Río Mataje, 01°13'00"N, 78°34'01"W, alt. 150 m, 14 Feb. 2000, *Neill* 12453 (UC); Esmeraldas, San Lorenzo, further along trail to Rio Mataje (beginning at point where collecting ended previous day), Awá encampment from Rio Palaví encampment, 01°07'N, 78°37'W, alt. 200–230 m, 11 Feb. 1988, *Hoover* 3935 (UC).

Habitat and ecology – *Cyclodium chocoense* is similar to *C. trianae* concerning habitat and ecology. Both species occur in primary or secondary wet evergreen forests, but *C. chocoense* seems to be often associated to rivers, and has a wider range of elevation, between 0–1750 m (vs. 100–1150 m). It is frequently recorded as terrestrial, but there are records of hemiepiphytic (*Alverson* 143) and epiphytic (*Forero* 4813) habits, whereas *C. trianae* seems to be exclusively terrestrial.

Conservation assessment – According to the IUCN categories and criteria (IUCN 2001), *C. chocoense* is considered least concern (LC). Although the species is threatened by area of occupancy (AOO), its extent of occurrence (EOO) is large (265,668.199 km²), far exceeding the 20,000 km² threshold for the vulnerable category under criterion B1. Even so, a large part of that extension comprises the Pacific Ocean. Its AOO, is estimated at 192.000 km², but it is largely under-estimated because of the species having been under-collected. Considering its wide EOO, its wide altitudinal range and the ecology of the species, a more accurate estimation of its AOO would be likely higher than the 2,000 km², the threshold for any threatened categories. As neither of B1 or B2 is met, *C. chocoense* is assessed as being least concern.

Notes – *Cyclodium chocoense* has been considered as a variety of *Cyclodium trianae* (besides the autonymic type variety) because, like that species, it has 2-pinnate laminae and somewhat reniform indusia (Smith 1986). We found, however, that these two taxa can be separated by a set of morphological characters that include degree of laminar division, number of sori, and dissection of the ultimate segments (fig. 5). The main differences are presented in the key below. Besides morphology, both species also have distinct patterns of distribution, as discussed in Distribution section. Our preliminary phylogenetic analysis (Bohn et al., in prep.) also recovered each taxon as monophyletic (three accessions of each were included), further supporting the recognition of *C. chocoense* as a distinct species. Furthermore, the existence of two morphologically distinct populations, in the east and western sides of the Andes, also suggests that they could be treated at the species level. Moran (1995) estimated that ca. 24% of the pteridophyte flora does not cross the physical barrier of the Andes, even though nearly all species are wind-dispersed. This creates an east-west pattern of distribution that is reflected in some morphological traits. This pattern has been recorded for species of *Alsophila* (Moran 1995), *Asplenium* (Murakami & Moran 1993), *Bolbitis* (Moran 2016), *Cyathea* (Moran 1991b), *Huperzia* (Øllgaard 1988), *Microgramma* (as *Solanopteris*; Moran 1992), *Stigmatopteris* (Moran & Labiak, 2016), and *Trichomanes* (Moran 1995).

Key to the species of *Cyclodium* with free venation

1. Laminae 1-pinnate-pinnatisect or more divided; indusia peltate, at least a few of them with a sinus, looking somewhat reniform……..……... 2

1’. Laminae 1-pinnate to 1-pinnate-pinnatifid; indusia always peltate……. 4

2. Rhizome scales to 3 mm long, dark brown to black, cordiform, folded lengthwise at center, and overlapping; several multicellular, acicular, translucent hairs on costae and rachis..... *C. seemannii*

2'. Rhizome scales 5–10.5 mm long, golden to brown, linear to lanceate, planar and not overlapping; without multicellular, acicular, translucent hairs on costae and rachis……. 3

3. Proximal pinnae pair 2-pinnate-pinnatifid; usually more than ten rows of sori between the base and apex of each segment; segment margins crenate to pinnatifid……..... *C. trianae*

3'. Proximal pinnae pair 1-pinnate-pinnatisect to 2-pinnate; usually less than nine rows of sori between the base and apex of each segment; segment margins entire or slightly crenulate at apex…….....……. *C. chocoense*

4. Costae with scales more than two cells wide at their bases……..…. 5

4'. Costae lacking scales……..……..…..... 6

5. Fertile fronds 25–34 cm long; proximal pinnae less than 1 cm wide; one row of sori between costae and margins; perine of spores lacking folds…...……..….. *C. rheophilum*

5'. Fertile fronds larger than 34 cm; proximal pinnae more than 1 cm wide; 2–5 rows of sori between costae and margins; perine of spores with conspicuous folds……… *C. guianense*

6. Rhizome scales ovate-lanceolate, bicolorous; lateral pinnae 11–25 pairs; indusia non-ciliate…… *C. alansmithii*

6'. Rhizome scales lanceate, concolorous; lateral pinnae 9–16 pairs; indusia ciliate……... *C. inerme*

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Figure 1 -- *Cyclodium alansmithii*: A, Habit with detail of abaxial side of rachis; B, Detail of a fertile pinna; C, Detail of free venation; D, Detail of adaxial side of rachis groove with bacilliform hairs; E, Top view of peltate indusium; F, Transversal view of peltate indusium and sporangia; A--F from *Tillet* 44942 (NY, US).

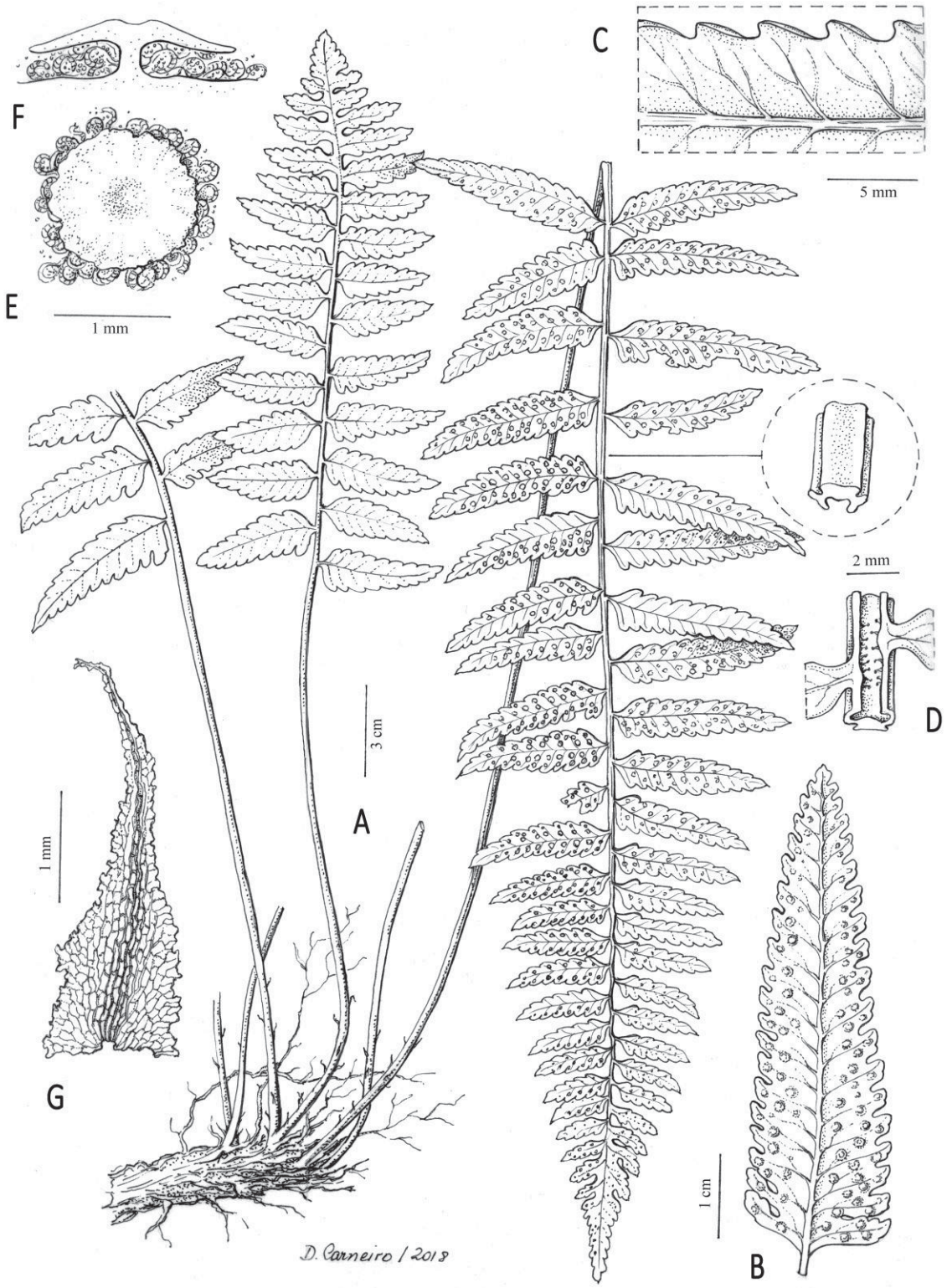


Figure 2 -- Pinna stalk, costa, indusium and scale of *Cyclodium alansmithii*: A, Pinna stalk with hairs; B, Costa with microscales; C, Frontal view from indusium; D, Petiole scale; B & D from *Zartman* 9172 (NY); A & C from *Henkel* 2174 (CAY).

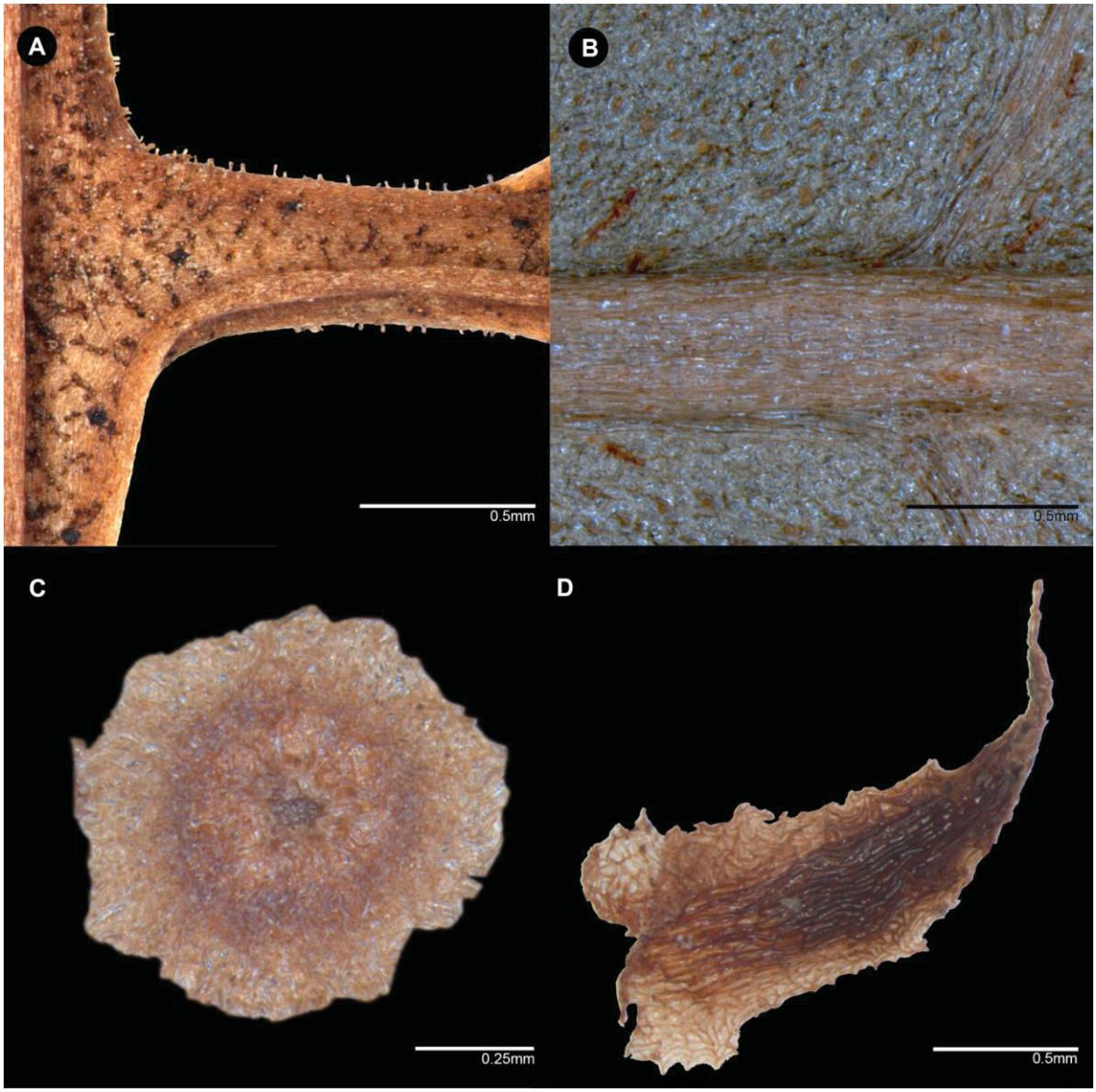


Figure 3 -- Spores, microscales and trichomes of *Cyclodium alansmithii*: A, Spore; B, Spore without perispore; C, Microscales; D, Bacilliform hairs of pinna stalk; A--D from *Zartman* 9172 (NY).

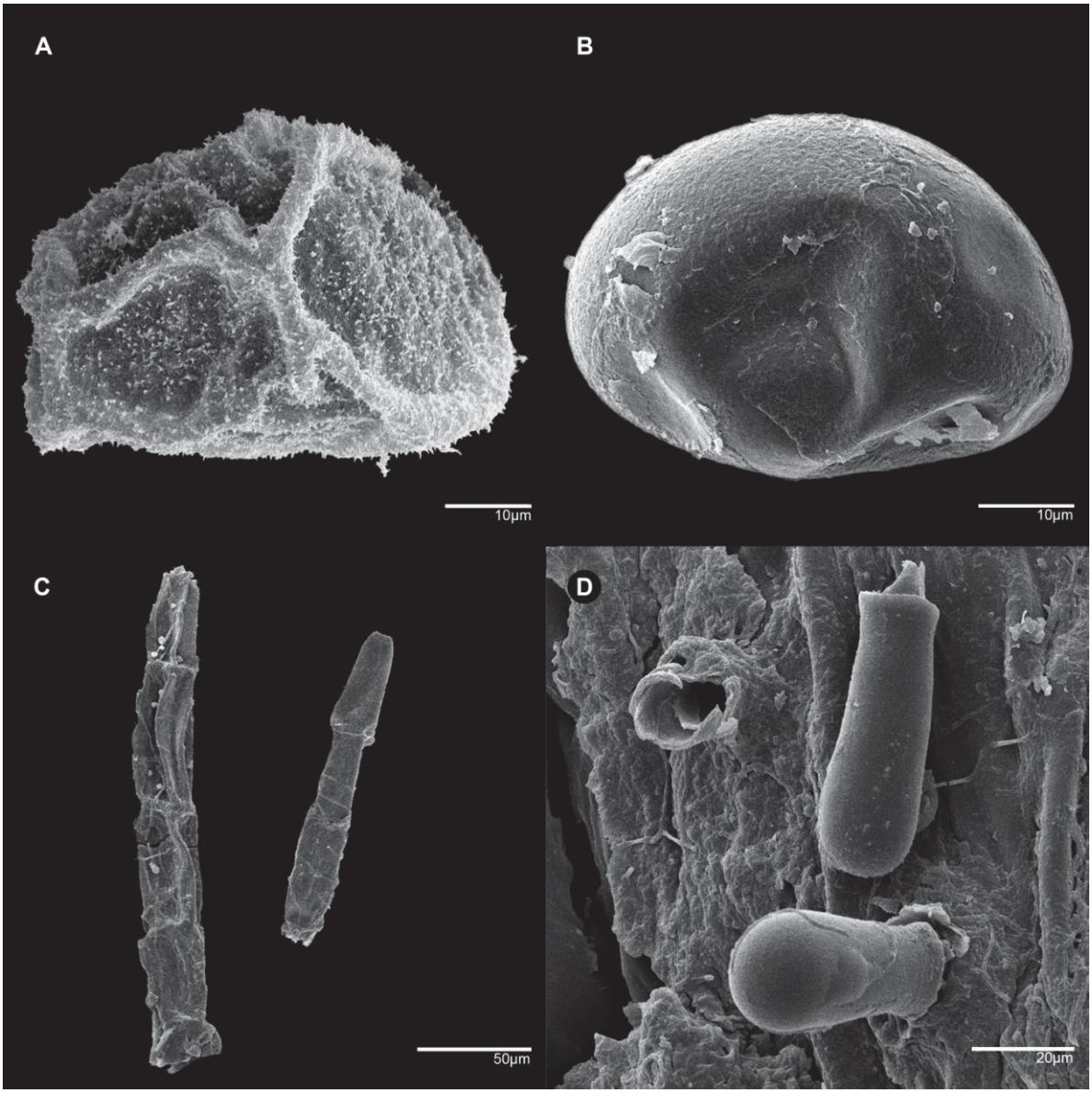


Figure 4 -- Clinal variation and geographic distribution of *Cyclodium alansmithii,* and *Cyclodium inerme*: A & C, Clinal variation and distribution of *C. alansmithii*; B & D Clinal variation and distribution of *C. inerme*; Images of *C. alansmithii* from *Henkel* 2174 (CAY), *Hoffmann* 2248 (CAY), *Maguire* 23525 (NY), *Steyermark* 75376 (US), *Tillet* 44942 (NY); Images of *C. inerme* from *Aymard* 6116 (UC), *Costa* 383 (RB), *Cremers* 5697 (CAY), *Froes* 26025 (UC), *Henicka* 293 (NY), *Hoff* 6719 (CAY), *Irwin* 54523 (NY), *Maas* 5891 (NY), *Maia* 441 (INPA), *Rivero* 2347-A (UC).

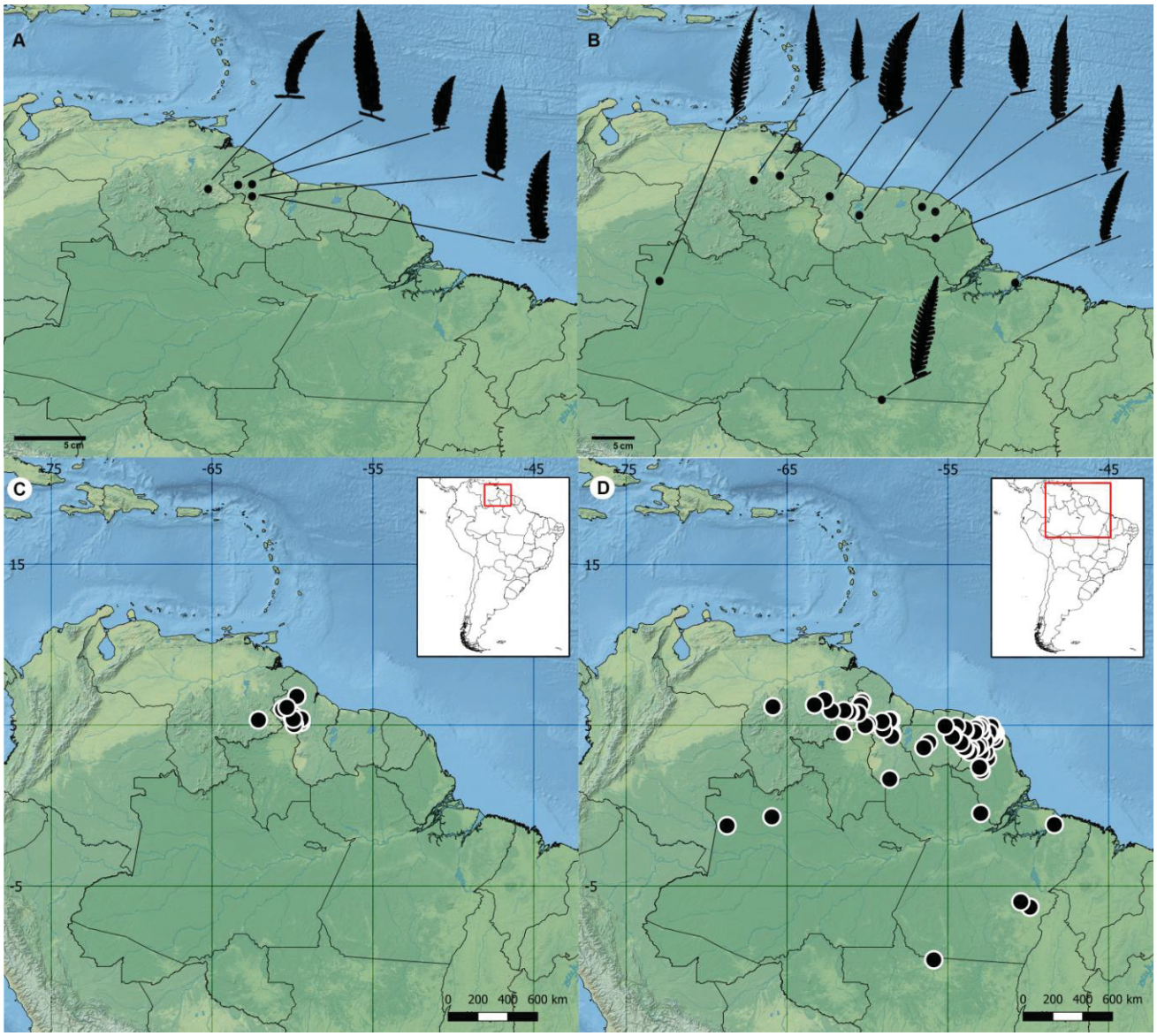
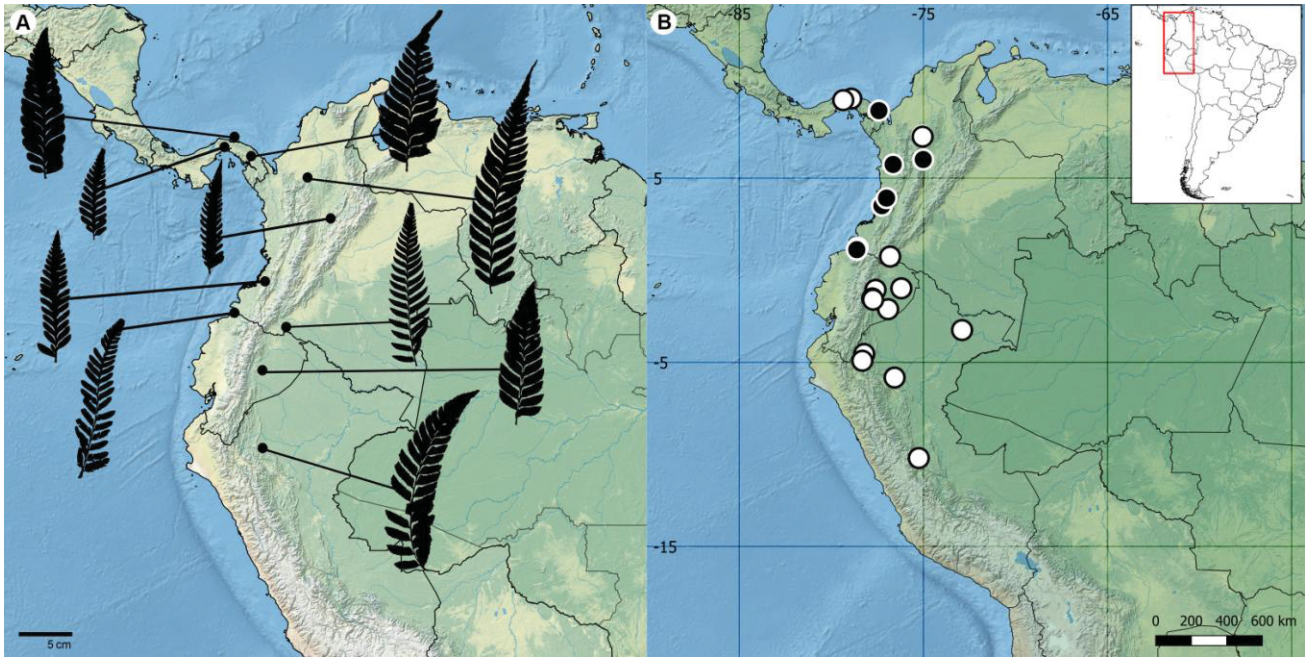


Figure 5 -- Clinal variation and geographic distribution of *Cyclodium chocoense* and *Cyclodium trianae*. A, Clinal variation of *C. chocoense* (left), and *C. trianae* (right); B, Distribution of *C. chocoense,* and *C. trianae*; Images of *C. chocoense* from *Forero* 1342 (NY), *Hoover* 3935 (UC), *Monsalve* 433 (UC), *Pittier* 4415 (US), *Valdespino* 289 (UC); Images of *C. trianae* from *Alberlaéz* 198 (NY), *Foster* 9498 (NY), *Herrera* 339 (UC), *Rodríguez* 6865 (NY), *Tuomisto* 11910 (UC).



CAPÍTULO 3 – Taxonomy of the fern genus *Cyclodium* (DRYOPTERIDACEAE)

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Abstract.

We provide a taxonomic revision for *Cyclodium*, a leptosporangiate fern genus that belongs to the polybotryoid clade of Dryopteridaceae. The genus can be distinguished from other members of the polybotryoid ferns by having dimorphic fronds and peltate indusia. *Cyclodium* is entirely Neotropical, occurring mainly in the northern portion of South America, especially in the Guianas, Venezuela, Amazon, and western portion of the Andes. We recognize 13 species, including **Cyclodium pubescens** Bohn & Labiak, which is here newly described. Lectotypes are designated for **Aspidium confertum**, **A. guianense**, **Cyclodium rigidissimum**, **Dryopteris callophylla**, and **Polystichum inerme**. Six species of *Cyclodium* are endangered, one is vulnerable, and the other specimens are least concern. *Cyclodium rheophilum* was categorized as data deficient. We provide morphological descriptions, maps, identification key, illustrations, and comments for all species.

Keywords: Biodiversity; Guianas; Neotropics; polybotryoids;

Cyclodium C.Presl is a neotropical fern genus in the Dryopteridaceae. It was originally described by Presl (1836) to accommodate three species: *Cyclodium confertum* (*Aspidium confertum* Kaulf.), *C. glandulosum* (*A. glandulosum* Blume), and *C. meniscioides* (*A. meniscioides* Willd.). However, subsequent authors changed its circumscription, such as Hooker (1862) and Hooker & Baker (1867), who treated it as a section of *Aspidium*, and Kuntze (1891) and Morton (1939), who placed *Cyclodium* under *Dryopteris* Adans. Christensen (1913; 1920) also considered *Cyclodium* under *Dryopteris,* and included three species (*D. guianensis*, *D. sancti-gabrieli*, and *D. varians*) in *Dryopteris* subg. *Stigmatopteris* group *Peltochlaena*, and *Dryopteris trianae* (Mett.) Kunze (=*Cyclodium trianae* (Mett.) A.R.Sm.) in a subgroup of *Polystichopsis*, along with species that now belong to *Arachniodes* Blume, *Polystichopsis* (J.Sm.) Holttum and *Lastreopsis* Ching.

The most recent and comprehensive taxonomic study on *Cyclodium* was published by Smith (1986), who recognized 10 species and four varieties. Since then, not much was done in terms of taxonomical novelties, but the genus has been included in several floras and regional checklists, such as Mickel (1985) for Trinidad, Cremers et al. (1993) for the Guianas, Tryon et al. (1991) for Peru, Smith (1995) for Venezuelan Guayana, Smith & Moran (1995) for Mesoamerica, Mori et al. (1997) for French Guiana, Peña-Chocarro et al. (1999) for Mbaracayú district of Paraguay, Naverrete (2001) for Amazonian Ecuador, Murillo-Pulido et al. (2008) and Forero & Gentry (1989) for Colombia, and Bohn et al. (2019) for Brazil.

Morphologically, *Cyclodium* is characterized by dictyostelic rhizomes, numerous vascular bundles in the stipe, 1-2 pinnate fronds (rarely simple or more divided), rachises with grooves more or less continuous onto the pinnae adaxially, chartaceous to subcoriaceous laminae, peltate or subpeltate (somewhat reniform) indusia, monolete and bilateral spores with a folded and echinulated perine, and $x = 41$ (Smith, 1986). Most of its species are terrestrial occurring in shaded places, from sea level to 800 m in elevation (Smith, 1986). However, some species were recorded as epiphytic, root climber, epipetric, and rheophytic (Smith, 1986). The terrestrial habitat has been recovered as the ancestral condition within the polybotryoid clade by Moran & Labiak (2015).

Hybridization seems to be an important process in the diversification of *Cyclodium*. Besides the intrageneric hybrids mentioned by Smith (1986), there are two intergeneric hybrids that were recently described from Brazil, each involving a cross of *C. meniscioides* with different species of *Polybotrya* (Engels & Canestraro, 2017; Schwartsburd et al., 2018).

Cyclodium occurs in Panama, Trinidad, French Guiana, Suriname, Guyana, Venezuela, Colombia, Ecuador, Peru, Bolivia, Paraguay, northern Argentina, and Brazil

(Smith, 1986; Tryon et al., 1991; Cremers et al., 1993; Smith & Moran, 1995; Kessler et al., 2018; Bohn et al., 2019) (Fig. 1). The Guianas are considered the center of diversity for the genus, where seven of the 13 species occur, and where almost all natural intrageneric hybrids were found (Smith, 1986).

Molecular phylogenetic studies have supported the recognition *Cyclodium*, and its close relationship with the polybotryoid clade within the Dryopteridaceae. Besides *Cyclodium*, the polybotryoid clade include the genera *Maxonia* C.Chr., *Olfersia* Kunze, *Polybotrya* Humb. & Bonpl. ex Willd., and *Polystichopsis* (J.Sm.) C.Chr. (Moran & Labiak, 2015). This clade is also supported by ecological and morphological characters, such as the root climber habit and dimorphic fronds (Moran & Labiak, 2015). More recently, Bohn et al. (in prep.) performed a molecular phylogeny using five plastid markers (*rbcL*, *rps4-trnS*, *trnG-trnR*, *psbA-trnH*, and *trnP-petG*). Their analyses included 24 assessions of *Cyclodium*, representing 78.6% of the species and varieties proposed by Smith (1986). They recovered *Cyclodium* as monophyletic and sister to *Polybotrya*, corroborating the results of previous studies (e.g., Schuettpelz & Pryer 2007; Moran & Labiak, 2015; Liu et al., 2016; Moran & Labiak 2016). Based on the phylogenetic studies by Bohn et al. (in prep.), some taxonomic modifications were also proposed. Most importantly, a new species, *Cyclodium alansmithii* Bohn & Labiak, was described (Bohn et al., in press); *C. trianae* var. *chocoense* was raised to the species level and is now recognized as *C. chocoense* (Bohn et al., in press); and *C. heterodon* var. *abbreviatum* was synonymized under *C. heterodon* (Bohn et al., in prep.). Furthermore, the following species were recovered as monophyletic: *Cyclodium calophyllum, C. heterodon, C. inerme, C. meniscioides, C. trianae* var. *trianae, C. trianae* var. *chocoense.*

In this study we present a taxonomic revision for *Cyclodium*, providing morphological descriptions, a key to the species, illustrations, maps of geographic distribution, conservational status and comments about the species. We recognized 13 species of *Cyclodium,* five lectotypes were selected, and one new species was described.

Methods

We examined a total of 686 specimens from the following herbaria: CAY, INPA, MBM, NY, P, RB, RON, UC, UFP, UPCB and US (Thiers 2019). Additional images of specimens and types were examined through online plataforms such as JSTOR Global Plants (https://plants.jstor.org), Reflora (http://reflora.jbrj.gov.br/), and SpeciesLink (http://splink.cria.org.br/). To avoid citing a large number of specimens from the same locality

only one specimen was selected and cited in the "specimens examined" list. An index of collector's names and numbers, including all specimens examined for this study, is provided (Appendix 1). In the morphological descriptions, the smallest and largest leaf on each specimen were measured for length and width. We used the basal pinnae to measure the division of laminae, as well as for the number of veins and sori. Measurements of hairs and scales were made using a stereomicroscope (AmScope 3TX). Images of hairs, scales, microscales, and indusium where made with an optic microscope (LEICA MZ16), with a coupled camera (LEICA DFC 500). In order to examine the perine ornamentation, spores were transferred with dissecting needles from herbarium specimens to aluminum stubs coated with asphalt adhesive. The stubs were then sputter-coated with gold for 2 min, and spores were imaged digitally using a JEOL JSM-6360LV scanning electron microscope at the Electron Microscopy Center of Universidade Federal do Paraná, Brazil. The dichotomic key was partially adapted from Bohn et al. (in press).

Information about the geographical distribution was obtained from herbarium labels or estimated according the main locality with Google Earth. When necessary, geographical coordinates were converted using the SpLink conversor tool (http://splink.cria.org.br/conversor). The maps of geographic distribution were made using the QGIS software (QGIS Development Team, 2013). Shape files were obtained from Organization for Flora Neotropica (www.nybgpress.org), and a raster file (1: 10,000,000) from Natural Earth (www.naturalearthdata.com). To calculate the conservation status, we used the GeoCAT (Bachman et al., 2011) tool, with 2 km of cell width. The results were analyzed according to the IUCN Red List categories and criteria (IUCN, 2001).

Results

We recognize 13 species of *Cyclodium*. Most of them occur in shaded places of evergreen forests, frequently associated to creeks, from "terra firme" to floodable, sandy or more rarely clay soil. The species are often terrestrial, but some (e.g. *C. akawaiorum, C. meniscioides, C. heterodon*) have been recorded as root climbers (terrestrial and with creeping rhizomes climbing when encountering trunks), ascending up to 2 m, or epipetric (e.g. *C. alansmithii, C. guianense, C. rheophilum*). The distribution, illustrations and spores of species are presented in Figs. 1–8, and a list of collectors is presented in Appendix 1.

Cyclodium pubescens Bohn & Labiak is here described as a new species. We synonymized *C. meniscioides* var. *paludosum* and *C. meniscioides* var. *rigidissimum* in *C.*

meniscioides sensu lato. The variety *C. heterodon* var. *abbreviatum* was synonymized in *C. heterodon*. A total of five lectotypes were designated for *Aspidium confertum*, *A. guianense*, *Cyclodium rigidissimum*, *Dryopteris callophylla*, and *Polystichum inerme*.

Considering the conservation status, most species were classified as least concern (LC), except for two species that were considered near threatened (NT) (*C. alansmithii* and *C. seemannii*), one that was considered vulnerable (VU) (*C. akawaiorum*), and another that was considered endangered (EN) (*C. rheophilum*).

Taxonomic Treatment

Cyclodium C.Presl, Tent. Pterid. 85. 1836. *Aspidium* sect. *Cyclodium* (Presl) Hooker, Sp. Fil. 4: 36. 1862. Lectotype (chosen by J. Smith, Hist. Fil. 203. 1875): *Aspidium confertum* Kaulf. [=*Cyclodium meniscioides* (Willd.) C.Presl var. *meniscioides*].

Dryopteris subg. *Stigmatopteris* (C.Chr.) C.Chr. group *Peltochlaena* Fée ex C.Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math. Afd. VII. 10: 74. 1913. Lectotype (chosen by A.R. Smith, Amer. Fern J. 76(2): 73. 1986): *Dryopteris subobliquata* (Hook.) Kuntze [=*Cyclodium inerme* (Fée) A.R.Sm.].

Peltochlaena Fée, Mém. Foug., Gen. Fil., 289. 1852. nom. illegit. Type: "*Peltochlaena nephrodiiformis"* Fée.

Plants terrestrial, root climbers or epipetric; *rhizomes* short to long-creeping, 0.3–1.5 cm diam., with ca. 1–20 fronds per 3 cm, scaly; *rhizome scales* basifixed, lanceate to lanceolate or ovate, 0.5–15 × 0.1–1.5 mm, concolorous or bicolorous, golden to black, sometimes with a darker center, margins entire, glandular, dentate or fimbriate; *fronds* monomorphic to dimorphic, lanceolate to elliptic, sterile fronds 16–150 × 3.5–47 cm, fertile fronds 23.5–184 × 6.5–47 cm; *petioles* stramineous to dark brown, with scales more abundant towards the base, and linear, septate, dark brown microscales, sometimes with bacilliform, translucid, yellowish hairs, 3–59 cm long in sterile fronds, 9.5–105.5 cm long in fertile fronds, 0.8–8 mm diam.; *petiole scales* basifixed with sinus or peltate, ovate or lanceate to lanceolate, sometimes appressed, 1–12 × 0.2–3 mm, concolorous or bicolorous, golden to dark brown, sometimes with a darker center, margins dentate to fimbriate; *laminae* 1-pinnate to 3-pinnate, rarely simple, chartaceous to coriaceous, with 3–25 pairs of lateral pinnae, conform or pinnatifid apex, 7–60 cm long in sterile fronds, 13–111.5 cm long in fertile fronds; *rachises* stramineous

to tan, sometimes flexuous, grooved adaxially, the grooves glabrescent, or with bacilliform, translucid, yellowish hairs, ca. 0.1 mm long, abaxially glabrous or with linear, septate, dark brown microscales and hairs similar to those of the grooves, sometimes with lanceate, brown scales, ca. 1–6 mm long; *pinnae stalks* 0.5–8 mm long, with bacilliform, translucid, yellowish hairs, and microscales similar to those of the rachis; *pinnae* linear to lanceolate or elliptic, bases cuneate to truncate and larger acroscopically, or asymmetric, truncate acroscopically and cuneate basiscopically, sometimes with a subauricule or an auricule, apices acute to acuminate or round, margins entire to pinatissect, sterile basal pinnae 1–25 × 0.3–7 cm, fertile basal pinnae 2.5–26 × 0.4–8.5 cm, sterile medial pinnae 3.8–19 × 0.4–6.5 cm, fertile medial pinnae 2.6–23 × 0.3–4 cm; *costae* abaxially glabrescent or with septate, linear, brown microscales, sometimes with lanceate scales, ca. 1–2 mm and bacilliform, translucid, yellowish hairs, ca. 0.1 mm long; *laminar tissue* glabrescent or with microscales similar to those on the costa, rarely with acicular, multicellular, translucid hairs; *veins* free or anastomosed, conspicuous or inconspicuous, when free 1–12 pairs per segment, when anastomosed 1–8 rows between costa and margin, sometimes the basal veinlets united with free tips or united to the next veinlets, rarely with a comissural vein; *sori* discrete or confluent, impressed or not, medial on veins, forming 1–12 rows between costa and margin, biseriate between two main lateral veins; *indusia* peltate or subpeltate, circular or somewhat reniform, ca. 0.3–2.5 mm diam, concolorous or bicolorous, stramineous to brown, sometimes with darker or lighter margins, the margins entire or ciliate, rarely with ciliate surfaces; *spores* 35–75 × 28–58 µm, the perines perforated or not, broadly folded, rarely without folds, densely echinulated, sometimes forming anastomoses, the folds low or high and continuous. $x = 41$.

Key to the species of *Cyclodium*

1. Veins anastomosing ……..……2
   2. Lamina apex pinnatifid …….....…….3
      3. Fronds hemidimorphic, sterile at the base and fertile at the apex; costa abaxially with scales composed of 2–3 cells at the base, up to 0.1 mm wide…….....…*C. heterodon*
      3. Fronds monomorphic or holodimorphic; costa abaxially with scales composed of more than 3 cells at the base, ca. 0.3 mm wide..……*C. calophyllum*
   2. Lamina apex conform …..…….…...……..4

4. Pinna margins with a comissural vein…….. ……..……*C. akawaiorum*

4. Pinna margins without a comissural vein…..……5

5. Rhizome scales dark brown to black, usually with twisted apices; basal pinnae of sterile fronds with 1–2.5 cm wide…….……*C. varians*

5. Rhizome scales golden to dark brown, without twisted apices; basal pinnae of sterile fronds up to 3 cm wide…….6

6. Rachis, costa and lamina pubescent, the hairs spreading, acicular, multicellular, and translucid……..…….……*C. pubescens*

6. Rachis, costa and lamina glabrous or with scales only...….....*C. meniscioides*

1. Veins free ……..……...……..7

7. Laminae 1-pinnate-pinnatisect or more divided; indusia peltate or subpeltate ….……8

8. Rhizome scales up to 3 mm long, dark brown to black, cordiform; rachis and costae with several multicellular, acicular, translucid hairs ……...……..*C. seemannii*

8. Rhizome scales 5–10.5 mm long, golden to brown, linear-lanceate; rachis and costae without multicellular, acicular, translucid hairs……....9

9. Basal pinnae 2-pinnate-pinnatifid; usually more than ten rows of sori between the base and apex of each segment; margin of segments crenate to pinnatifid……*C. trianae*

9. Basal pinnae 1-pinnate-pinnatisect to 2-pinnate; usually less than nine rows of sori between the base and apex of each segment; margin of segments entire or slightly crenulate at apex……...*C. chocoense*

7. Laminae 1-pinnate to 1-pinnate-pinnatifid; indusia peltate only……...…..…….10

10. Costae with at least few scales…...……....11

11. Fertile fronds 25–34 cm long; basal pinnae with less than 1 cm wide; one row of sori between the costa and the margin; perine of spores lacking folds……*C. rheophilum*

11. Fertile fronds larger than 34 cm; basal pinnae with more than 1 cm wide; 2–5 rows of sori between the costa and the margin; perine of spores with conspicuous folds……...*C. guianense*

10. Costae lacking scales……..…….……...……..12

12. Rhizome scales ovate-lanceolate, bicolorous; 11–25 pairs of lateral pinnae;

indusia non-ciliate.……..……..*C. alansmithii*

12. Rhizome scales lanceate, concolorous; 9–16 pairs of lateral pinnae; indusia ciliate……..…....*C. inerme*

1. Cyclodium akawaiorum A. R. Sm., Amer. Fern J. 76(2): 71, f. 6. 1986. Type: Guyana. Roraima: NW facing slopes of Mt. Roraima, vicinity of Camp 6, near the end of the Waruma Trail, ca. 1 mi N of the prow, 5°16'30"N, 60°44'45"W, [1280–1310] m, 27 Mar 1978, *J. F. Warrington, K. Burras, J. R. Woodhams & P. J. Edwards K.E.R. 76* (holotype: UC-1484715]; isotype: K, n.v.). (Figs. 1A, 3D–G, 7A).

Plants terrestrial or root climbers; r*hizomes* long-creeping, 0.6–1.5 cm diam., with ca. 2–4 fronds per 3 cm, scaly; *rhizome scales* basifixed, lanceate to lanceolate, 5–10.5 × 0.4–1 (–1.5) mm, concolorous or bicolorous, golden to brown, sometimes with a darker center, margins minutely to strongly dentate; *fronds* subdimorphic to dimorphic, lanceolate, sterile fronds 43–57 (–71.5) × 12–22 cm, fertile fronds 23.5–63 (–107.5) × 9–16 cm; *petioles* stramineous to dark brown, with several scales more abundant towards the base and sometimes with septate, linear, dark brown microscales, 15–25 cm long in sterile fronds, 21–32 (–48) cm long in fertile fronds, 1.5–3 (–6) mm diam.; *petiole scales* basifixed with a narrow sinus, lanceate to lanceolate, 2–7 (–10.5) × 0.3–1.5 mm, concolorous or bicolorous, golden to dark brown, sometimes with a darker center, margins dentate to fimbriate; *laminae* 1-pinnate, subcoriaceous to coriaceous, with 8–15 pairs of lateral pinnae, gradually reduced to a conform apex, sometimes with a subauricule at base, 22–33 (–47) cm long in sterile fronds, 23.5–27 (–35) cm long in fertile fronds; *rachises* stramineous to tan, sometimes flexuous, grooved adaxially, the grooves with bacilliform, translucid, yellowish hairs, ca. 0.1 mm long, abaxially glabrous or with linear, septate, dark brown microscales and hairs similar to those of the grooves, sometimes with lanceate, brown scales, composed of few cells at base, ca. 1–2 mm long, with dentate margins; *pinnae stalks* 3–6 mm long, with bacilliform, translucid, yellowish hairs, and microscales similar to those of the rachis; *pinnae* linear to lanceolate, bases cuneate to truncate and larger acroscopically, or truncate acroscopically and cuneate basiscopically, apices acute to acuminate, sometimes rounded, margins entire to crenulate, sterile basal pinnae 6.5–11 (–15) × 1.7–2.2 (–3.5) cm, fertile basal pinnae 5–6 (–9) × 0.5–1.1 (–1.7) cm, sterile medial pinnae 6–9.5 (–11.5) × 1.6–2 (–3) cm, fertile medial pinnae 4–6.5 (–

9) × (0.3–) 0.7–1 (–1.5) cm; *costae* abaxially with linear, septate, dark brown microscales, and rarely with lanceate scales, composed of few cells at base, ca. 1–2 mm; *laminar tissue* with microscales similar to those of costa; *veins* anastomosed, conspicuous, with 1–3 anastomoses between costa and margin, sometimes the basal veinlets united with the tips free or united to the next veinlets, the veins projected at the end, forming a comissural vein; *sori* discrete or confluent near costa, impressed, medial on veins, forming 1–3 rows of sori between costa and margin, biseriate between two main lateral veins; *indusia* peltate, circular, ca. 1–2.5 mm diam, concolorous or bicolorous, stramineous to brown, sometimes with darker margins, the margins entire or ciliate; *spores* 44–56 × 28–30 µm, the perines perforated, broadly folded and densely echinulated, the folds low and continuous.

Distribution, ecology and conservation status.—Cyclodium akawaiorum is known from Guyana and Venezuela (Bolívar). The species is often recorded as a root climber on tree trunks in montane rain forests, between 670–1500 m. The type specimen indicates that juvenile plants grow on the floor, until the rhizomes find a climbing support. However, some specimens were recorded as epiphytic (*Boom 8931; Boom 8942; Clarke 9150; Clarke 10414; Hahn 5424*). *Henkel* 4321 was registered as "terrestrial to subepiphytic", suggesting that this species is a root climber (sensu Canestraro et al., 2014). The extent of occurrence (EOO) of *C. akawaiorum* is 7,892 km², which is less than the threshold of 20,000 km² of the vulnerable category (VU) under criterion B1a, bi. Although the area of occupancy (AOO) was estimated as 44 km², which would suggest it as being "endangered" (EN), only one criterion was met (B2bii). Considering that this species occurs in a non-populated area, near to the National Parks of Canaima (VEN), Monte Roraima (BR) and Kaieteur (GUY), *C. akawaiorum* is accessed here as "vulnerable".
VU B1a, bi.

Specimens examined. GUYANA. Cuyuni–Mazaruni: Top of waterfall above Kako River, 5°36'53.2"N, 60°42'4.9"W, 677 m, 18 May 2009, *Wurdack et al. 5061* (NY); ± 2 km NW of northern tip of "prow" of Roraima, 5°15'N, 60°35'W, 1000–1500 m, 23 Feb 1989, *Hahn & Gopaul 5424* (CAY); Riverine rain forest, on E side of the Waruma river (a tributary of the Kako & Mazaruni rivers), NNW of the N prow of Mt. Roraima, 5°21'20"N, 60°45'50"W, [518] m, 1 Apr 1978, *Warrington et al. 167* (UC); N–W facing slopes of Mt. Roraima, vicinity of Camp 6 (near the end of the 'Waruma Trail'), N of the 'prow' W,

5°16'30"N, 60°44'45"W, 1280–1310 m, s.d. [collected from cultivation on 9 Jul 1980], *Warrington et al. K.E.R. 1207* (K, UC); Upper Mazaruni River region, Karowtipu Mountain, 5°45'N, 60°35'W, 920 m, 17 Apr 1987, *Boom & Gopaul 7412* (NY); Upper Potaro River region, Wokomung base camp and vicinity, 5°05'N, 59°50'W, 1070–1160 m, 29 Jun 1989, *Boom & Samuels 8931* (NY); Idem, *Boom &*Upper Potaro River region, Wokomung base camp and vicinity, 05°05'N, 59°50'W, 1070–1160 m, 29 Jun 1989, *Boom & Samuels 8942* (NY). **Potaro–Siparuni:** Mt. Ayanganna, east face, plateau above first escarpment, 2 km N of camp, 5°20'0920'9"N, 59°56'46"W, 1100 m, 14 Jun 2001, *Clarke et al. 9150* (CAY); Pakaraima Mts, Mt. Wokomung, Wusupubaru Creek, 2 km from juncture with Suruwabaru Creek, 5°03'N, 59°53'W, 975–1125 m, 13 Feb 1993, *Henkel et al. 1372* (CAY); Pakaraima Mts, Mt. Wokomung, W slope on sub–plateau near head of Mo–toy–mabaru Creek, 5°04'N, 59°53'W, 1150–1200 m, 11 Nov 1993, *Henkel et al. 4269* (CAY, NY, US); Pakaraima Mts, Mt. Wokomung, NE facing slopes above second of four escarpments, 5°5'55.9"N, 59°50'15.6"W, 1400 m, 1 Jul 2003, *Clarke et al. 10414* (US); Ibid., 5°04'N, 59°53'W, 1000–1100 m, 12 Nov 1993, *Henkel et al. 4321* (CAY); Pakaraima Mts, Mt. Wokomung, toe slope 0.5–2 km NW from northern escarpment, 5°04'N, 59°53'W, 1300–1400 m, 13 Nov 1993, *Henkel et al. 4349* (CAY). **VENEZUELA. Bolivar:** Northwestern slopes of Cerro Venamo, southeast of camp 125, [5°59'51"N, 61°24'38"W], 1200 m, 14 Apr 1960, *Steyemark & Nilsson 124* (US); Mt. Roraima Paikwa Trail, on tree trunk, [5°09'16"N, 60°47'28"W], [1402] m], 28 Oct 1973, *Persaud 110* (NY).

The isotype of *C. akawaiorum* (K) was already indicated with doubt by Smith (1986), probably because it was a specimen collected under a project conducted by Kew Gardens. Although we decided to maintain this material in the protologue, we were unable to find it. However, we found *K.E.R. 1207,* a specimen cultivated at Kew and cited as "Collected as sporelings. Small fronds coll. 11/1979. Large frond collected 9/1982" in the same locality that the holotype.

Cyclodium akawaiorum can be recognized by its 1–pinnate fronds, coriaceous texture, conform apical pinna, and anastomosing veins. It is more similar to *C. meniscioides*, from which it differs by thicker laminae (coriaceous vs. chartaceous to subcoriaceous), less areoles between costa and margin (1–3 vs. 4–7 rows), and the presence of a marginal comissural vein. Some specimens have flexuous rachises (*Henkel 1372*; *Henkel 4349*; *Boom 8931* and *8942*), but we were not able to correlate this character to any other differences in morphology or

distribution. Notwithstanding, this character seems to be plastic in this species: it occurs in one duplicate of *Henkel 4349* whereas in *Henkel 4349* it does not. The phylogeny of Bohn et al. (in prep.) shows that *C. akawaiorum* is sister to *C. meniscioides,* a relationship that was previously mentioned by Smith (1986) on the basis of morphology. Strongly dimorphic fertile–sterile fronds and conform apical pinnae are synapomorphies to this clade.

2. Cyclodium alansmithii Bohn & Labiak, (in press). Type: Guyana. Upper Mazaruni River Basin, Mt. Ayanganna, [5°22'03"N, 59°56'52"W], 800 m, 27 Jul 1960, *S. S. Tillett, C. L. Tillett & R. Boyan 44942* (holotype: NY-02859537; isotype: MO-1858729 n.v., US-00719099]). (Figs. 1B, 5, 7B).

Plants terrestrial or epipetric; *rhizomes* short–creeping, 0.3–0.5 (–1) cm diam., with ca. 6–10 fronds per 3 cm, scaly at apex; *rhizome scales* basifixed, ovate–lanceolate, 3–5 × 0.5–1 mm, bicolorous, brown, with thinner, lighter margins, these entire to slightly erosed; *fronds* monomorphic to subdimorphic, lanceolate to elliptic, sterile fronds (31–) 37.5–50 (–63) × 8.5–10.5 (–17) cm, fertile fronds (29,5–) 37–64.5 (–80) × (8–) 10–14 cm; *petioles* stramineous to tan, with scattered scales, rarely with septate, linear, brown microscales, 11–18 (–36) cm long in sterile fronds, 16.5–36.5 (–48) cm long in fertile fronds, 1.5–3 mm diam.; *petiole scales* basifixed with a sinus or peltate, ovate–lanceolate, appressed, 1.5–5 × 0.5–3 mm, bicolorous, brown, with thinner, lighter margins, these entire to slightly fimbriate; *laminae* 1–pinnate pinnatifid, chartaceous, with (11–) 15–25 pairs of lateral pinnae, sometimes overlapped towards apex, and gradually reduced to a pinnatifid apex, (18–) 23.5–32.5 cm long in sterile fronds, (13–) 17.5–34 cm long in fertile fronds; *rachises* stramineous to tan, grooved adaxially, the grooves with bacilliform, translucid, yellowish hairs, ca. 0.1 mm long, abaxially glabrous or with septate, linear, brown to dark brown, scattered microscales, rarely with brown scales, ca. 1.5–2 cm long; *pinnae stalks* 1.5–3 (–4) mm long, with bacilliform, translucid, yellowish hairs and microscales similar to those of the rachis; *pinnae* linear to elliptic, bases truncate, sometimes with a subauricule acroscopically, apices acute to round, margins undulate or crenate to pinnatifid margins, more dissected in fertile fronds, sterile basal pinnae (3.8–) 4.5–8 × 1.3–2 cm, fertile basal pinnae (2.5–) 3.5–6 (–8) × (0.7–) 1–1.4 (–2) cm, sterile medial pinnae 3.8–5.3 (–7) × 1.1–1.6 cm, fertile medial pinnae (2.6–) 3–6 × 0.7–1.6 cm; *costae* abaxially with linear, septate, brown to dark brown microscales; *laminar tissue* glabrescent, with microscales similar to those of costa; *veins* free, conspicuous, 3–4

furcate between costa and margin, the basal veins ending below or immediately above sinus, rarely reaching the margin; *sori* discrete, impressed, medial on veins, forming 2–3 (–4) rows of sori between costa and margin, biseriate between two main lateral veins; *indusia* peltate, sometimes with the stalk slightly dislocated from center, circular, ca. 0.5–1 mm diam, concolorous, stramineous, entire to erose margins; *spores* 47–55 × 37–40 µm, the perines with few perforation, broadly folded and densely echinulated, the folds low and continuous.

Distribution, ecology and conservation status.—Cyclodium alansmithii occurs from Guyana to Venezuela. Most specimens are terrestrial, but some have been recorded as epipetric. This species is often associated to creeks and hillsides, growing on sandstone soil, between 170–1400 m. One accession (*Gillespie 2288*), is unusual because it occurs on "terra firme" forests, at 70–75 m. As discussed by Bohn et al. (in press), *C. alansmithii* was considered as "endangered" under criteria B2a, bii.
EN B2a, bii

Specimens examined. GUYANA. Cuyuni-Mazaruni: Below 1st escarpment (of four) of Kamakusa Mt., 0-1.5 mi. SW of Micrandra (4th) Camp, 5°51'08"N, 60°11'17"W, 840 m, 29 May 2012, *Wurdack et al. 5749* (CAY); Kako River, Chinakuruk Mountain, cliff foot of mountain, [5°31'47"N, 60°42'39"W], 1226 m, 21 May 2009, *Redden et al. 6709* (NY); At headwaters of Kangu River, W branch; ± 4 km NW of E peak of Mt. Ayanganna. First talus slope of plateau, 5°25'N, 60°00'W, 700 m, 5 Mar 1987, *Pipoly et al. 11045* (US); Upper Mazaruni River Basin, [5°22'03"N, 59°56'52"W], 800 m, 27 Jul 1960, *Tillett et al. 44942* (NY, US). **Potaro-Siparuni:** Upper Kuribrong River, 5°34'20"N, 59°54'22"W, 475 m, 20 Mar 2011, *Zartman et al. 9172* (INPA); Marina Falls, 5°22'43"N, 59°28'93"W, 449 m, 28 Mar 2011, *Zartman et al. 9359* (INPA); Mt. Ayanganna, east face, camp at base of first of four escarpments, 5°22'22"N, 59°57'34"W, 1120 m, 16 Jun 2001, *Clarke et al. 9199* (NY); Potaro River Gorge, [5°10'59"N, 59°28'00"W], 17 May 1944, *Maguire & Fanshawe 23525* (NY). **VENEZUELA. Bolívar:** Chimantá Massif, Southwestern-facing forested slopes of Chimantá-tepuí (Torono-tepuí) between Base Camp and steep slopes above valley of Río Tirica, [5°18'43"N, 62°07'23"W], 1000–1400, 15 May 1953, *Steyemark 75376* (US).

Cyclodium alansmithii is characterized by its ovate–lanceolate, bicolorous scales, 1–pinnate laminae, pinnae with truncate bases and crenate margins, and free veins. This species

is similar to *C. inerme*, but *C. alansmithii* occurs only in Guyana and Amazonian Venezuela, whereas *C. inerme* has a wider distribution from Amazonian Venezuela and Brazil, Guyana, Suriname, and French Guiana. *Cyclodium alansmithii* can be distinguished from *C. inerme* by its ovate–lanceolate and bicolorous rhizome scales (vs. lanceate and concolorous), reduced fronds (the measurements overlap, but *C. alansmithii* is typically smaller overall), pinna bases truncate on both sides (vs. truncate acroscopically, cuneate basiscopically), non–ciliate indusia (vs. ciliate), and spores with perforated perines (vs. non–perforated). *Cyclodium alansmithii* was recovered as sister to *C. inerme* by Bohn et al. (in prep.), and the absence of costal scales on costae abaxially supports this clade.

3. Cyclodium calophyllum (C. V. Morton) A. R. Sm., Amer. Fern J. 76(2): 73, f. 7A–D. 1986. *Dryopteris calophylla* C. V. Morton, Bull. Torrey Bot. Club 66(1): 49. 1939. Type: Colombia. Santander: Vicinity of Barranca Bermeja, Magdalena Valley, between Sogamoso and Colorado Rivers, 100–500 m, 4 Sep 1934, *O. L. Haught 1353* (**lectotype, here designated**: US-00067163; isolectotypes: GH-00342738, MICH-1190409, US-00067161, US-00067162]). (Figs. 1A, 3H–J, 7C).

Plants terrestrial; *rhizomes* long–creeping, ca. 1.5 cm diam., with ca. 2–4 fronds per 3 cm, scaly; *rhizome scales* basifixed, lanceolate, 2–5 × 0.5–1.5 mm, concolorous, dark brown to black, margins entire; *fronds* monomorphic to subdimorphic, lanceolate to elliptic; sterile fronds 70–75 × 25–26 cm, fertile fronds 104–116 × 31.5–38 cm; *petioles* stramineous to dark brown, with scattered scales more abundant towards the base, and septate, linear, dark brown microscales, sometimes with bacilliform, translucid, yellowish hairs, 28–30 cm long in sterile fronds, 40.5–56 cm long in fertile fronds, 5–6 mm diam.; *petiole scales* basifixed with a sinus, lanceate to lanceolate, 4–10 × 0.5–1 mm, concolorous, light brown, margins dentate; *laminae* 1–pinnate, chartaceous to coriaceous, with 10–14 (–18) pairs of lateral pinnae and pinnatifid apex, 42–45 cm long in sterile fronds, 50.5–63.5 (–73.5) cm long in fertile fronds; *rachises* tan, with bacilliform, translucid, yellowish hairs, and septate, linear, golden microscales, also with lanceate scales, ca. 1–6 mm long, concolorous, golden to brown, margins dentate; *pinnae stalks* (2–) 4–6 mm, with bacilliform, translucid, yellowish hairs, and linear, septate, microscales, also with lanceate scales similar to those from rachis; *pinnae* linear to elliptic, bases truncate acroscopically and cuneate basiscopically, asymmetric at the base with a subauricule or auricule at the acroscopic side, apices acute and crenate to serrate, margins

crenate to pinnatifid, sterile basal pinnae 12–14 × 2–4 cm, fertile basal pinnae 14–18.5 × 1.7–2.4 cm, sterile medial pinnae 10–13 × 1.5–2 cm, fertile medial pinnae 13.5–15.5 × 1.4–1.8 cm; *costae* abaxially with linear, golden scales, some of them with few cells at base, and linear, septate, golden microscales; *laminar tissue* with microscales similar to those of the costae; *veins* highly variable, free to anastomosing, conspicuous, sometimes with just one or two pairs of veinlets united ending in lamina below sinus or running to sinus, the remaining veinlets ending before margin; *sori* discrete, not impressed, medial on veins, forming ca. 4–6 rows of sori between costa and margin, biseriate between two main lateral veins; *indusia* peltate, circular, ca. 1–1.5 mm diam, bicolorous, brown with a blackish center, entire margins; *spores* 57–75 × 42–58 µm, the perines perforated, broadly folded and densely echinulated, forming anastomosing areoles, the folds high and continuous.

Distribution, ecology and conservation status.—Cyclodium calophyllum is known from Venezuela, to Colombia, Peru, and Brazil (for the two latter, first record). The species is terrestrial, sometimes associated to stream margins, occurring in evergreen forests, between 100–500 m. One specimen (*Aymard 4862*) is unusual because it occurs on the tepuis, between 850–1100 m. The extent of occurrence (EOO) of *C. calophyllum* is 2,490,388 km², which includes it as "least concern" by GeoCAT. The area of occupancy (AOO) was estimated at 36 km², below the threshold of 500 km² of the endangered category (EN) under the criterion B2a, bi. Considering that this species occurs in a small range of altitude and has a small area of occupancy regards the large extent of occurrence, this species is accessed as being "endangered".

EN B2a, bi

Specimens examined. BRAZIL. Mato Grosso: Vila Bela da Santissima Trindade: Fazenda Cabixi, junto ao Rio Cabixi, ca. 12 km da divisa com Rondônia, 13°S, 60°10'10'W, 11–14 Jan 1987, *Prado & Salino 18* (UC). **COLOMBIA. Santander:** Vicinity of Barranca Bermeja, Magdalena Valley, between Sogamoso and Colorado Rivers, [7°12'19"N, 73°48'39''W], 100–500 m, 4 Sep 1934, *Haught 1353* (US); Catatumbo, Campo Tibú, [8°28'18"N, 72°55'08"W], 200 m, 16 May 1959, *Bischler 2461* (COL). **PERU. Loreto:** Loreto: About 2 km N of the village San Antonio at lower Río Marañon, 4°32'S, 73°38'W, 100–200 m, 15 Jan 1996, *Tuomisto et al. 8113* (UC). Maynas: R. B. Alpahuayo-Mishana, [3°58'25"S, 73°33'33"W], 122 m, 23 Nov 2000, *Flores A. 1602* (NY); Upper Río Itaya, about

5 km SSE of the village Carbajal, 4°19’S, 73°35’W, 100–200 m, 5 Mar 1996, *Tuomisto et al. 10068* (UC). **VENEZUELA. Bolivar:** Sifontes: Bosques húmedos primarios, em la base de los tepuyes (Paraitepuy y Guytepuy) del sector “La Hoyada” (Paraitepuy), 7 km al N-W del Caserío “El Pilón”, 58 km al W de Sta. Elena de Uairén, 4°40’N, 61°33’W, 850–1100, 23 Oct 1986, *Aymard C. 4862* (UC); Selvas húmedas del Rio Oris, a la altura de “Los Picachos”, 6°8’N, 63°55’W, 175 m, 13 Apr 1987, *Stergios 10604* (UC). **Zulia:** 6 km east north east of Río de Oro, 9°06’N, 72°50'W, 100–350 m, 28 Mar 1982, *Liesner & González 13307* (UC).

The protologue of *Dryopteris calophylla* C. V. Morton cited three syntypes at US (“[accession] nos. 1662621–3”). In 1983–1984, Smith labelled one of these specimens (barcode US 00067163) as “Lectotype”, but, because this was not effectively published, the designation of a type was not achieved (Turland et al., 2018, Art. 7.10). In his monograph of *Cyclodium*, Smith (1986) cited the same three syntypes at US (“[holotype]: US, 3 sheets!”) without choosing a lectotype. Because there is nothing indicating that these syntypes are parts of a single specimen, they must be treated as duplicates from among which a lectotype must be chosen (Turland et al., 2018, Art. 8.3). We chose US [barcode] 00067163 as lectotype because it is the only fertile syntype at US.

Cyclodium calophyllum can be distinguished by its 1–pinnate laminae, pinnatifid apex, irregularly anastomosing veins and presence of conspicuous scales on costae abaxially. It mostly resembles *C. guianense,* which differs by having subdimorphic laminae, anastomosing veins, and spores with perforated perines. It is also similar to *C. meniscioides*, from which it differs by having rhizome scales with margins entire (vs. dentate to fimbriate), more pairs of lateral pinnae (10–18 vs. 3–8), and pinnatifid apices (vs. conform). Smith (1986) indicated that *C. calophyllum* is a possible intermediate between *C. guianense* and *C. meniscioides*. The specimens from Brazil and Peru have more entire pinnae and less areoles between costa and margin. Bohn et al. (in prep.) found that *C. calophyllum* (*Prado & Salino 18*, from Brazil *Flores 1602,* from Peru) is monophyletic and sister to a clade with *C. guianense* and *C. rheophilum. Cyclodium meniscioides* forms a clade with *C. akawaiorum*, and this clade is sister to *C. calophyllum* + (*C. guianense* + *C. rheophilum*). Besides that, considering some new records, *C. guianense* and *C. meniscioides* overlaps the distribution of *C. calophyllum* in some regions, such as Brazil (Mato Grosso), Peru (Loreto), and Venezuela (Bolívar).

4. Cyclodium chocoense (A. R. Sm.) Bohn. & Labiak, Plants Ecology and Evolution (in

press.). *Cyclodium trianae* var. *chocoense* A. R. Sm., Amer. Fern J. 76(2): 93, f. 13G. 1986. Type: Colombia. Chocó: Corcovada region, upper Río San Juan; ridge along Yeracüí Valley, 200–275 m, 24–25 Apr 1939, *E. P. Killip 35287* (holotype: US-01050249; isotype: COL-000006256]). (Figs. 1C, 4N–R, 7D).

Plants terrestrial; *rhizome* short–creeping, 1–1.5 cm diam., with ca. 6–7 fronds per 3 cm, scaly; *rhizome scales* basifixed, linear to lanceate, 5–10 × 0.2–0.4 (–0.6) mm, concolorous, brown to golden, apices somewhat twisted, margins entire; *fronds* monomorphic, lanceolate–ovate, sterile fronds 48.5 × 11.5 cm, fertile fronds 80.5–97 (–129) × 14–30 cm; *petioles* stramineous to dark brown, with scales more abundant towards the base, also with septate, linear, brown microscales and bacilliform, translucid, yellowish hairs, 21 cm long in sterile fronds, (22–) 45–76 cm long in fertile fronds, 2.5–5 mm diam.; *petiole scales* basifixed with a sinus, lanceate, 4–7 × 0.5–1 mm, concolorous, brown to dark brown, margins entire; *laminae* 1–pinnate–pinnatifid to 2–pinnate, subcoriaceous to coriaceous, with 13–16 (–21) pairs of lateral pinnae and apex pinnatifid, 27.5 cm long in sterile fronds, 25–47.5 (–53) cm long in fertile fronds; *rachises* stramineous to tan, with septate, linear, dark brown, scattered microscales and sometimes with linear to lanceate, brown scales, with few cells at base, 0.5–1 mm long; *pinnae stalks* 3–8 mm long, with bacilliform, translucid, yellowish hairs and microscales similar to those of the rachis; *pinnae* lanceolate to elliptic, with 7–11 pairs of lateral pinnules, bases asymmetric, with the first segment larger and arising acroscopically, apices pinnatifid, sterile basal pinnae 7.5 × 2.3, fertile basal pinnae 8.5–10 × 2.3–4.7 cm, sterile medial pinnae 6 × 1.5, fertile medial pinnae 7–13 × 1.5–4 cm; *costae* abaxially with scales and microscales similar to those of the rachis; *laminar tissue* scales and microscales similar to those of the costa; *pinnules* lanceolate to elliptic, bases truncate acroscopically and frequently attached to costae basiscopically, apices acute or round and sometimes crenate, margins entire to slightly undulate, 1.5–2.2 × 0.5–0.6 cm; *costules* with scales and microscales similar to those of the costa; *veins* free, conspicuous, 6–12 furcate between costa and margin, or when the veinlets arising from the main veins 1–furcate, ending below margin basiscopically, and shorter, ending on sori acroscopically; *sori* discrete, not impressed, terminal on veins, forming 6–12 rows of sori between costa and margin, biseriate between two main lateral veins; *indusia* subpeltate to peltate, ca. 1 mm diam, concolor, stramineous to tan, entire to undulate margins sometimes ciliate; *spores* 44–56 x 28–30 µm, the perines non–perforated, broadly folded and densely echinulated, the folds low and

continuous.

Distribution, ecology and conservation status.—*Cyclodium chocoense* is known from Panama, western Colombia (east to Cordillera Central) and western Ecuador (first record). It shows a Mesoamerican–Chocó distribution pattern that is found in many other groups of ferns as *Asplenium* (Muramaki & Moran, 1993), *Lellingeria* (Labiak, 2013), *Lomariopsis* (Moran, 2000), and *Megalastrum* (Moran & Prado, 2010). All specimens are terrestrial occurring in wet evergreen forests, between 0–1750 m, sometimes associated to rivers. One specimen was recorded as epiphytic (*Forero 4813*). As discussed at Bohn et al. (in press), *C. chocoense* was assessed as "least concern".
LC

Specimens examined. COLOMBIA. Antioquia: Anorí: Vereda Puntiadero o la Concha abajo, quebradas El Salto y El Claro, sector la Concha abajo, 7°17'01.2"N, 75°05'17.1"W, 720 m, 16 Jan 2004, *Rodríguez et al. 4461* (COL). Mutatá: Finca El Dárien, [7°14'47"N, 76°26'00"W], 200 m, 18 May 1976, *Atehortúa & Hoyos 216* (HUA); Corregimiento Longaní, margem derecha del Rio Longaní, 2 km al norte de Mutatá, [7°14'21"N, 76°26'03"W], 80–100 m, 19 Nov 1987, *Alberláez et al. 248* (HUA). San Luis: Vía Medellín-Bogotá, Quebrada La Tebaída, 6°8'N, 75°10'W, 1010–1060 m, 22 Jun 1987, *Callejas et al. 4002* (HUA, NY). Planta Providencia: 26 km S & 23 km W (air) of Zaragoza, in valley of rio Anorí between dos Bocas & Anorí, 7°13'N, 75°03'W, 400–700 m, 2 Mar 1977, *S. White et al. 140* (HUA); Ibid., 7°13'N, 75°03'W, 400–700 m, 13 Jun 1976, *Sheperd 432* (HUA); 28 km SW of Zaragoza, valley of Río Anorí in aread surronding the confluence of Quebrada La Tirana and Río Anorí, approx. 3 km upriver from Plant Providencia, 7°18'N, 75°04'W, 400–700 m, 4 Mar 1977, *Alverson et al. 143* (HUA, NY). **Bajo Calima:** Buenaventura: Secretaria de Agicultura, [3°59'47"N, 76°58'35"W], 80 m, 31 Mar 1984, *de Escobar et al. 4000* (HUA). Ibid., [3°59'47"N, 76°58'35"W], 70 m, 1 Apr 1984, *de Escobar & Folsom 4025* (HUA). **Caldas:** Sanamá: El Carmén, 05°31'36"N, 75°02'26"W, 7 May 1992, *B. César 6973* (HUA). **Cauca:** Timbiquí: East side of Gorgona Island, dense forest along stream, [2°49'58"N, 77°42'24"W], 50–100 m, 11 Feb 1939, *Killip & Garcia 33172* (COL). **Chocó:** Bahía Solano: Dense forest along Quebrada Jella, near ciudad Mutis, [6°12'34"N, 77°18'08"W], 0–75 m, 21-23 Feb 1939, *Killip & Garcia 33622* (COL); km. 11 between El Valle and ciudad Mutis, [6°13'47"N, 77°22'54"W], 50 m, 15 Feb 1986, *Wood 5296* (COL);

Low hills behind the beach 1-1.5 km NW of El Valle, N of the lagoon, [6°07'48"N, 77°26'26"W], 25–75 m, 13 Feb 1971, *Lellinger & de la Sota 343* (COL); Near Punta San Francisco Solano, ca. 10 km NE of Puerto Mutis (Bahía Solano), [6°14'40"N, 77°23'15"W], 10–100 m, 27 Jan 1971, *Lellinger & de la Sota 82* (HUA); NW side of Alto del Buey, trail along ridge from the confluence of the forks of the rio Mutatá above Río Dos Bocas toward the top of Alto del Buey, [6°08'08"N, 77°19'38"W], 950–1450 m, 8-10 Feb 1971, *Lellinger & de la Sota 211* (HUA); Ibid., [6°08'08"N, 77°19'38"W], 1450–1750 m, 9 Feb 1971, *Lellinger & de la Sota 253* (COL). Canton Del San Pablo: pan american Highway (under construction), ca. 10 km W of las Animas, [5°17'41"N, 76°41'01"W], 100 m, 12 Jan 1979, *Gentry &. Renteria A. 24057* (COL). Condoto: Carretera Andagoya-Condoto, cerca de Andagoya, 5°06'N, 76°40'W, 14 Apr 1979, *Forero et al. 5288* (COL). Istmina: Dense forest near junction of Rio Condato and rio San Juan, [5°05'50"N, 76°41'47"W], 100–150 m, 20 Apr 1939, *Killip 35084* (COL). Río Bicordó, arriba de Noanamá, orillas del rio, 4°42'N, 76°55'W, 6 Apr 1979, *Forero et al. 4753* (COL); Rio El Salto (tributary of the Río Suruco), 9 km W of Andagoya, [5°05'32"N, 76°44'17"W], 75–100 m, 23 Feb 1971, *Lellinger & de la Sota 478* (COL); Río Fujiadó, afluente del Río San Juan, 4°36'N, 76°54'W, 7 Apr 1979, *Forero et al. 4813* (COL). Litoral Del Bajo San Juan: Region del río Pichimá, comunidad indigena Waunana, 4°25'N, 77°17'W, 23 Nov 1976, *Forero 746* (COL). Nóvita: Quebrada Máncamo, afluente del Rìo Tamaná, cerrito em la margen izquierda, 4°57'N, 76°38'W, 11 Apr 1979, *Forero et al. 5051* (COL). Nuqui: Corregimiento Termales, Quebrada Piedra Piedra, [5°42'32"N, 77°15'55"W], 0–25 m, 6 Sep 1994, *Acevedo-Rodriguez et al. 6807* (HUA). Quibdó: Carretera Quibdó-Tutunendo, 15 km de Quibdó, [5°43'39"N, 76°36'10"W], 45 m, 6 Sep 1976, *Forero & Jaramillo 2528* (COL); Margem izquierda del río Munguidó, afluente del río Atrato, en pequeno cerro cerca de Altagracia, [5°42'38"N, 76°46'27"W], 50 m, 4 May 1975, *Forero et al. 1535* (COL); Río Serrano, afluente del río Atrato, 4-6 km arriba del Guayabal, [5°44'37"N, 76°38'37"W], 50 m, 29 Apr 1975, *Forero et al. 1342* (COL, NY). Tadó: Corcovada region, upper Río San Juan, ridge along Yeracüí Valley, [5°20'15"N, 76°15'05"W], 200–275 m, 25-26 Apr 1939, *Killip 35287* (COL); Mojarras de Tadó, 8.5 km E of Istmina, [5°16'14"N, 76°33'04"W], 150–250 m, 20 Feb 1971, *Lellinger & de la Sota 417* (COL). Unión Panamericana: Quebrada Peña Negra, 8 km W of Quidbó-Istmina road on new Pan American Highway, [5°17'04"N, 76°39'33"W], 90 m, 10 Jan 1979, *Gentry & Renteria E. 23937* (COL, HUA). **Nariño:** Barbacoas: Al W de El Diviso, [1°22'40"N, 78°13'59"W], 350 m, 3 Jun 1973, *Leist 2158* (COL); Carretera Barbacoas-Junin, km 8, [1°32'58"N, 78°05'44"W], 140 m, 18 Dec 1972, *Hagemann & Leist 1702* (COL). San Andres de Tumaco: Km 80, [1°45'33"N,

78°47'07"W], 300 m, 1 Nov 1967, *Mora 4222* (COL). **Valle del Cauca:** Buenaventura: About 18 km east of Buenaventura, dense forest, [3°53'56"N, 76°58'58"W], 50 m, 14 Feb 1939, *Killip & Garcia 33246* (COL); Bajo Calima, [3°53'04"N, 77°00'39"W], 2 Apr 1984, *de Escobar 4061* (HUA); Bajo Calima, Concesión Pulpapel/Buenaventura, 3°55'N, 77°00'W, 100 m, 20 Sep 1984, *Monsalve B. 433* (UC); Corregimiento San Cipriano, Reserva Natural de Escalerete, bajando de la casa blanca, [3°55'59"N, 77°10'00"W], 100 m, 14 Apr 1993, *Cruz et al. 4044* (COL); Costa del Pacífico, río Cajambre, Quebrada del Corosal, [3°30'47"N, 77°14'03"W], 17 May 1944, *Cuatrecasas 17731* (UC); Dense forest near highway bridge over Río Dagua, about 20 km east of Buenaventura, [3°50'34"N, 76°47'26"W], 40 m, 15 Feb 1939, *Killip & Garcia 33320* (COL); Hoya del río San Juan: alrededores de Palestina, 4°10'N, 77°10'W, 5 m, 26 Mar 1979, *Forero et al. 4035* (COL); Quebrada Taparal, afluente del río San Juan, alrededores de la comunidad indigena Waunaná de Taparalito, 4°10'N, 77°10'W, 5–10 m, 28 Mar 1979, *Forero et al. 4269* (COL); Quebrada La Sierpe, afluente del Río San Juan, 4°10'N, 77°10'W, 5 m, 1 Apr 1979, *Forero & Jaramillo 4449* (COL); Ibid., 4°10'N, 77°10'W, 5 m, 1 Apr 1979, *Forero & Jaramillo 4450* (COL). Dagua: Agua Clara, along highway from Buenaventura to Cali, [3°44'50"N, 76°43'11"W], 100 m, 6 Jun 1944, *Killip & Cuatrecasas 38991* (US); Carretera Cali-Buenaventura, rio Danubio inferior, [3°43'38"N, 76°40'09"W], 200 m, 15 Sep 1967, *Hagemann 424* (COL). **ECUADOR. Esmeraldas:** San Lorenzo: Territorio Indígena Awá, Mataje village, 500 m west of Río Mataje, 01°13'00"N, 78°34'01"W, 150 m, 14 Feb 2000, *Neill et al. 12453* (UC); Further along trail to Rio Mataje (beginning at point where collecting ended previous day), Awá encampment from Rio Palaví encampment, 01°07'N, 78°37'W, 200–230 m, 11 Feb 1988, *Hoover et al. 3935* (UC). **PANAMA. Panama:** Cerro Azul: cabecera del río San Cristobal, [9°13'52"N, 79°21'02"W], 900 m, 28 Dez 1986, *Valdespino & Rios 289* (UC); Cerro Jefé, [9°13'58"N, 79°21'01"W], 16 Feb 1985, *van der Werff & van Hardeveld 6986* (UC). **San Blas:** Kuna Yala: Hills of Sperdi, near Puerto Obaldía, San Blas coast, [8°39'57"N, 77°25'05"W], 20–200 m, Sep 1911, *Pittier 4415* (US).

Cyclodium chocoense is characterized by its 1–pinnate–pinnatifid to 2–pinnate laminae, and free veins. Two specimens from Ecuador (*Hoover 3935*; *Neill 12453*) are unusual by having more dissected laminae than typical specimens from Colombia and Panama.

It has been considered a variety of *Cyclodium trianae* because, like that species, it has 2-pinnate laminae and a somewhat reniform indusia (Smith 1986). We found, however, that

these two taxa can easily be separated by a set of morphological characters that include degree of laminar division, number of sori, and dissection of the ultimate segments. Besides morphology, *Cyclodium trianae* is found only on the eastern side of the Andes, whereas *C. chocoense* occurs only on the western side (Bohn et al., in press)

Another similar species is *C. seemannii,* which differs by its cordiform, blackish rhizome scales, more dissected lamina, and presence of multicellular, acicular and translucid hairs on costa and rachis. The phylogeny presented by Bohn et al (in prep.) did not include *C. seemannii,* but different accessions of *C. chocoense* were recovered as monophyletic and sister to *C. trianae*.

5. Cyclodium guianense (Klotzsch) van der Werff ex L. D. Gómez., Phytologia 60(5): 371. May 1986. *Aspidium guianense* Klotzsch, Linnaea 20: 364. 1847. *Polystichum guianense* (Klotzsch) C. Presl., Epimel. Bot. 58. 1851 [as "gujanense"]. *Aspidium abbreviatum* Schrad. var. *guianense* (Klotzsch) Baker in Martius, Fl. Bras. 1(2): 464. 1870. *Dryopteris guianensis* (Klotzsch) Posth., Ferns Surinam 51. 1928. *Stigmatopteris guianensis* (Klotzsch) C. Chr., Index Filic., Suppl. 3: 174. 1934. *Cyclodium guianense* (Klotzsch) A.R. Sm., Amer. Fern J. 76(2): 75. Apr–Jun 1986*, nom. illeg. hom.* Type: Guyana, s.d., *M. R. Schomburgk 1157* (**lectotype, here designated**: B-200137414; isolectotypes: B-200137415; K-000590373; UC-416949).

Polypodium sancti–gabrieli Hook., Sp. Fil. 4: 233.1862. *Nephrodium sancti–gabrieli* (Hook.) Baker in Martius, Fl. Bras. 1(2): 469. 1870. *Dryopteris sancti–gabrieli* (Hook.) Kuntze, Rev. Gen. Pl. 2: 813. 1891. *Stigmatopteris sancti–gabrieli* (Hook.) C. Chr., Index Filic. Suppl. 3: 175. 1934. Type: Brazil. Amazonas: São Gabriel da Cachoeira, Feb 1852, *R. Spruce 2153* (lectotype, designated by Smith, 1986: K-000590374; isolectotypes: BM-000937905, BM-000937906; BR-0000006869885, BR-0000006870911; G-00348381 n.v.; P-00630605]). (Figs. 1D, 3R–T, 7E–G).

Plants terrestrial, root climber or epipetric; r*hizomes* short–creeping, 0.5–1.5 cm diam., with ca. 5–14 fronds per 3 cm, scaly; *rhizome scales* basifixed, lanceolate, 4–12 × 0.4–1.5 mm, concolorous, light to dark brown, margins entire to minutely denticulate; *fronds* monomorphic to subdimorphic, lanceolate to elliptic; sterile fronds 55–110 × 12–34 cm, fertile fronds 65–140 × (13–) 20–36 (46) cm; *petioles* stramineous to tan, sometimes darker at base, with scales more abundant towards the base, (12.5–) 20–47 cm long in sterile fronds,

(13–) 20–84 cm long in fertile fronds, 0.8–6 mm diam.; *petiole scales* basifixed with a narrow sinus, lanceate to ovate, 2–7 × 0.5–1.5 mm, concolorous or bicolorous, golden to light brown, with a somewhat darker center, margins entire to slightly dentate, more rarely fimbriate; *laminae* 1–pinnate to 1–pinnate–pinnatifid, chartaceous to subcoriaceous, with 16–23 pairs of lateral pinnae and apex pinnatifid, (23–) 30–60 cm long in sterile fronds, (22–) 30–64 cm long in fertile fronds; *rachises* stramineous to tan, grooved adaxially the grooves with bacilliform, translucid, yellowish, hairs, ca. 0.1 mm long, abaxially with lanceate, bicolorous, golden to brown scales or black and lighter margins, ca. 0.3–2 mm long, margins fimbriate, also with septate, linear, golden microscales; *pinnae stalks* 1–4 mm long, with bacilliform, translucent, yellowish hairs, and scales and microscales similar to those of the rachis; *pinnae* linear to lanceolate, sometimes elliptic, bases truncate, or truncate acroscopically and cuneate basiscopically, slightly asymmetric at the base with a subauricule at the acroscopic side, apices acute to acuminate and crenate to serrate, margins undulate to crenate, sterile basal pinnae 7–13.5(–17.5) × 1.2–2.5 (–3.1) cm, fertile basal pinnae 7–18 (–23) × 0.8–2.6 cm, sterile medial pinnae 7–17 × 1– 2.5 m, fertile medial pinnae 8–17.5 (–23) × 0.8–2.5 cm; *costae* abaxially with linear to lanceolate, brown scales, and linear, septate, light to dark brown microscales; *laminar tissue* glabrescent or with scales and microscales similar to those on the costa, often with yellow to reddish, resinous, circular excretions; *veins* free, inconspicuous, 3–5 furcate between costa and margin, the anterior basal one of each segment ending in lamina below sinus, the remaining veinlets ending near margin; *sori* discrete, impressed, medial on veins proximally to costa, medial or terminal on veins proximally to margin, forming 2–4 (–5) rows of sori between costa and margin, biseriate between two main lateral veins; *indusia* peltate, circular, ca. 0.3–1.5 mm diam, concolorous or bicolorous, stramineous with a darker center, entire to glandular margin; *spores* 35–65 × 33–52 μm, the perines non–perforated, broadly folded and slightly to densely echinulated, the folds high and continuous.

Distribution, ecology and conservation status.—Cyclodium guianense is distributed in French Guiana, Suriname, Guyana, Trinidad, Venezuela, Colombia, Brazil, and Bolivia. The occurrence in states Rondônia and Mato Grosso of Brazil represents new records. Most of specimens are terrestrial or epipetric, and frequently associated to creeks and highly humid ambient. It grows in evergreen forests, with sandy soil, 100–1300 m. The extent of occurrence (EOO) of *C. guianense* is 7,812,998 km², which includes it as “least concern” by GeoCAT. The area of occupancy (AOO) was estimated at 400 km², which is less than the threshold of

500 km² of the endangered category (EN), under criterion B2 bii. Considering that *C. guianense* has a large EOO, a wide altitudinal range and occurs in many different ecosystems, its AOO is more likely to exceed the threshold of 2,000 km² for any threatened categories. Thus, because only one criterion for the endangered category is met, *C. guianense* is assessed here as "least concern".

LC

Specimens examined. BOLIVIA. Cochabamba: Shinahota: [17°0'S, 65°13'59"W], 306 m, 2009, *Weigelt 90147* (GOET, LPB, TUR, Z). **Santa Cruz:** Velasco: Parque Nacional Noel Kempff M: Campamento Huanchaca, 13°54'S, 60°48'W, 650 m, 18 May 1994, *Arroyo et al. 716, 717* (MO, UC, USZ). **BRAZIL. Acre:** Projeto de Colonização Sta Luzia, a 45km de Cruzeiro do Sul da estrada Cruzeiro do Sul–Rio Branco (BR 364), 7°45'S, 72°15'W, 13 Sep 1985, *Jangoux et al. 85–34* (INPA). **Alagoas:** Ibateguara: Usina Serra Grande, Engenho Coimbra, Grota do Dudé, 09°00'03.00"S, 35°51'14.2"W, 390–415 m, 9 Feb 2001, *Pietrobom & Santiago 4822* (UFP, NY). Between Murici e Messias, Estação Ecológica de Murici, 09°11'05"S–09°16'48"S, 35°45'20"W–35°55'12"W, 100–650 m, 6 May 2009, *Pereira & Silva 1066* (UFP). **Amapá:** Rivière Haut Jari, [1°17'4.4"S, 53°31' 2.8"W], 400 m, 17 Aug 1993, *de Granville et al. 12328* (CAY, P). **Amazonas:** Manaus: Km 167, BR 174, Manaus–Caracaraí Road, [2°6'33"S, 59°59'34"W], 18 Sep 1974, *Prance et al. 22686* (INPA, NY). Presidente Figueiredo: Usina Hidrelétrica de Balbina, em trilha da grade do PPBio, aproximadamente 1h e 30m de barco, 20°13'45"S, 59°17'39"W, 4 Oct 2006, *Zuquim 237* (INPA). São Gabriel da Cachoeira: Rio Negro, vicinity of Base Camp, Cano Tucano, Rio Cauaburí, [0°8'15.7"S, 66°4'50.4"W], 125 m, 24 Nov 1965, *Maguire et al. 60279* (NY, UC). **Mato Grosso:** Aripuanã: ca. 37 km da MT 170, 4 km de Cidade Morena direção Juínia, 9°31'S, 60°30'W, 300 m, 10 Oct 1996, *Windisch 8603* (BHCB). Nova Canaã do Norte: Resgate de FLORA da UHE Colíder, Lote A de supressão. Floresta do "Planalto dos Parecís", 10°57'42"S, 55°45'29"W, 274 m, 17 Apr 2015, *Engels & Dias 3206* (MBM). **Pará:** Brejo Grande do Araguaia: Road BR 22, Capanema to Maranhão, vicinity of Cachoeira, km 96, [5°40'44"S, 48°19'13"W], 30 Oct 1965, *Prance & Pennington 1825* (NY, RB). Canaã dos Carajás: Floresta Nacional dos Carajás, Serra sul, corpo A, 6°18'36"S, 50°27'16"W, 582 m, 29 Jun 2010, *Marino et al. 2422* (BHCB). Goianésia: Zona de preservação da Vida Silvestre Base 4, Trilha 8, 04°15'0.6"–04°15'47"S, 49°31'01.7"–49°30'17.6"W, 102–179 m, 25 Sep 2008, *Fernandes & Maciel 299* (RB). Marabá: Coleta no acampamento azul, [5°25'45"S, 49°8'31"W], 24 May 1982, *Secco et al. 303* (NY). Paraupebas: Serra dos Carajás, AMZA

camp AZUL, an abandoned manganese exploration camp, 6°06'S, 50°17'W, 500–550 m, 31 May 1982, *Sperling et al. 5907* (NY). **Pernambuco:** Ibateguara: Usina Serra Grande, Engenho Coimbra, Grota do Taquarí/Porcos, 09°00'19"S, 35°51'50.8"W, 390–415 m, 10 Feb 2001, *Pietrobom & Santiago 4888* (UFP). Jaqueira: Usina Colônia, (Mata Córrego da Guariba), 08°43'0.2"S, 35°50'20.2"W, 652 m, 3 Apr 2002, *Lopes & Pietrobom 575* (MBM, UFP). Lagoa dos Gatos: RPPN Pedra D'Antas, [8°41'39"S, 35°51'22"W], 12 Aug 2012, *Farias et al. 34* (UFP). São Vicente Ferrer: Complexo do Maciço do Mascarenhas, "Mata do Estado", 07°35'00"S, 35°30'00"W, 304–394 m, 17 Aug 1998, *Pietrobom 4384* (MBM, UFP). Timbaúba: Complexo da Serra do Mascarenhas, Usina Cruangi, Engenho Água Azul, 07°36'47.5"S, 35°23'26.7"W, 304–394 m, 30 Jan 2001, *Pietrobom & Santiago 4759* (MBM, UFP). Vicência: Pedra Mole, Mata do Engenho Jundiá, [7°37'27"S, 35°19'56"W], 24 Aug 1961, *Tavares 765* (UFP). **Rondônia:** Espigão do Oeste, 11°31'S, 61°00'W, 260 m, 10 Dez 2006, *da Costa 33* (UPCB). **Roraima:** Cantá: Upper slopes of Serra da Lua, 2°25-29'N, 60°11-14'W, 1200 m, 24 Jan 1969, *Prance et al. 9452* (NY). Caracaraí: Parque Nacional do Viruá, rio Baruana, em morro à esquerda da trilha perpendicular ao módulo do PPBio, [1°16'49"S, 61°0'47"W], 2 Dez 2006, *Carvalho & Nascimento 1093* (INPA). **COLOMBIA. Caquetá:** Solano: Upper Apaporis Basin, Rio Apaporis near the confluence of the Rios Ajaju and Macaya, cerro del Castillo, [0°6'54"N, 71°20'42"W], 548 m, 27 Jul 1943, *Schultes 5661* (US). **FRENCH GUIANA. Arrondissement of Cayenne: Camopi:** Embouchure de la rivière Grand Tamouri (affluent du Camopi) = Saut Bambaye, [2°52'19"N, 52°56'37"W], 15 Mar 1974, *de Granville 2123* (CAY). **Gros Montagne:** Mont Bakra – Région des Emérillons, 3°18'N, 52°57'W, 550 m, 15 Apr 1993, *Cremers 13114* (CAY, UC). **Regina:** Mont Chauve, 3°49'N, 52°44'W, 100 m, 19 Apr 1997, *Cremers & Crozier 15105A* (CAY). **Roura:** Montagne Tortue – Bassin de la Comté, 4°18'N, 52°28'W, 200 m, 2 Jun 1988, *Cremers 10063* (CAY). Saint-Ellie**:** Base camp at Pic Matécho, ca. 22.5 km NE of Les Eaux Claires, 3°45'N, 53°2'W, 500 m, 10 Sep 2000, *Mori & Smith 25094* (CAY, NY, P). **Saint-Laurent-du-Maroni: Mana:** Haute crique Baboune, affluent de la rivière Mana, [5°39'52"N, 53°46'36"W], 31 Jul 1981, *Cremers 7370* (CAY). **Maripasoula**: Montagne de l'inini, extrèmité NW, 3°30'40"N, 53°36'W, 550–600 m, 15 Aug 1985, *Cremers et al. 8913* (CAY, INPA). **Papaichton:** Monts Kotika, plateau latéritique sommital, 3°55'10"N, 54°11'10"W, 730 m, 21 Feb 2005, *de Granville et al. 16867* (CAY, UC). **Monts Atachi Bakka**: Mont Atachi Bacca, región de l'inini, plateau sommitale, 3°33'N, 53°55'W, 650 m, 16 Jan 1989, *Cremers et al. 10271* (CAY, UC, US). Paul-Isnard**:** Montagne Lucifer, sud du plateau sommital, Région de Paul-Isnard. Lucifer, bassin amont de la crique Reine, à 80 km au sud de

Saint-Laure, 4°46'N, 53°55'W, 500 m, 20 Nov 1999, *Boudrie et al. 3428* (CAY). **Saül:** Sentier Botanique, E of Eaux Claires, at one of the tributary streams of the St. Eloi River, 3°37'N, 53°12'W, 250 m, 1 Sep 1994, *Mori et al. 23753* (CAY). **GUYANA. Upper Takutu-Upper Essequibo:** Essequibo, Acarai Mts, Tinarnau Creek at NW'ern base of Tinarnau Peak, 1°16'N, 58°36'W, 500 m, 5 Mar 1994, *Henkel et al. 4970* (CAY). **SURINAME. Brokopondo:** Tafelberg, wet walls, cataract, lower north ridge, [4°39'51"N, 55°14'30"W], 19 Sep 1944, *Maguire 24815* (US). **Sipaliwini:** Amékan Tabiki: Nassau Mountains, Marowijne River, [4°47'60"N, 54°36'0"W], 400–550 m, 1 Jan 1955, *Maguire et al. 39064* (NY). Boven Coppename: Grace Camp, Tafelberg Mountain. Hardwood forest on north side of Grace Kreek camp, 1 km north of Grace Falls, 3°54'32"N, 56°12'44"W, 800–820 m, 4 Jul 1998, *Hawkins 1885* (NY). **TRINIDAD.** s.l., [10°21'33"N, 61°13'50"W], 1877–80, *Fendler 97* (NY, UC, US). **VENEZUELA. Amazonas:** Atabapo: Alto Rio Casiquiare,15 km al S-W de Tama Tama, 3°1'N, 65°57'W, 160 m, 6 Mar 1990, *Aymard & Delgado 8487* (UC). Alto orinoco: [2°45'43"N, 64°42'5"W], 3 Oct 1951, *Croizat 782* (NY). Atures: Base E del Cerro Cuao, Caño Piedra. 75 km SE de Puerto Ayacucho, 5°05'N, 67°19'W, 1050 m, Sep 1989, *Fernandes et al. 6169, 6174* (UC). Rio Negro: Neblina Base Camp of Río Bario (=Rio Mawarinuma), Lima de las Piñas (Pineapple Ridge), 1.5 km south of Neblina Base Camp, a saddle on upland trail, 00°49'15"N, 66°09'38"W, 215 m, 15 Feb 1985, *Beitel 85197* (NY). Mavaca: Rio Metacuni, pic 2, frente no. 4, selvas húmedas siempre-verdes de lomerío y ladera, faldas del Tepuy-Altiplanicie Sedukerawa y áreas ayacentes, 3°15'N, 64°56'W, 210–650 m, 26 Feb 1990, *Stergios & Velazco 14244-a* (UC). **Bolívar:** Barceloneta: Bosques a lo largo de la frontera Venezolano-Brasilera, noreste de la Serranía Pia-soi (Pia-shauhy, Pia-Savi), 3°53'N, 62°46'W, 650–800 m, 42891 Feb 1962, *Steyemark 90656* (NY). Canaima: Río Ataperé, sabanas de Guayaraca, camino hacia el Auyantepui, cuenca alta del Río Cucurital, 5°43'16"N, 62°32'21"W, 1150 m, 5 Nov 2002, *Rodríguez & Hokche 1603* (UC). Raúl Leoni: Asukupa (Los Frijoles), 16 km (por aire) al sur de Uriman, 5°15'N, 62°40'W, 0 m, Mar 1986, *Fernandez 2360* (UC). **Delta Amacuro:** East side of Río Cuyubini, vicinity of large granitic boulders, [8°6'55"N, 63°7'5"W], 100–200 m, 18 Nov 1960, *Steyemark 87654* (NY). **Táchira:** Uribante: Empresa Las Cuervas, near La Fundación, 8°50'N, 71°47'W, 900 m, 7 Jul 1983, *van der Werff & González 4990* (NY).

Smith (1986) indicated with doubt that the type of *Aspidium guianense* Klotzsch should be at B ("Type: Guyana, *Schomburgk 1157* (B?, not seen, isotypes: K!, UC!)"). It was

common practice in botany to assume that the holotype was always in the institution where the describing author was known to have worked. This practice, however, is not accepted by the rules if the current Code, which states that when a type is indicated by reference to an entire gathering consisting of more than one specimen, those specimens are syntypes (Turland et al., 2018, Art. 40, Note 1). There are two syntypes at B, from which we select B-200137414 as lectotype. For *Polypodium sancti–gabrieli* Hook., Smith (1986) listed the following information: "TYPE: Brazil, Amazonas, São Gabriel, *Spruce 2153* ([holotype] K!, isotypes BM!-2 sheets, BR!-2 sheets, G!, P!)". However, there is no holotype for this name because Hooker cited only a gathering (i.e., *Spruce 2153*) and did not specify a particular herbarium. Thus, instead of holotype, there are seven syntypes from which a lectotype may be designated (Turland et al., 2018, Art. 9.6). Being prior to 1 January 2001, when Smith (1986) cited the K specimen as "holotype", his action resulted in that specimen becoming the lectotype (under current Art. 9.10), even if this has never been his intention (see Prado et al. 2015).

Cyclodium guianense is characterized by its 1–pinnate fronds, free veins, and the presence of conspicuous scales on costa abaxially. All locations show a little variation of the pinna size, but in Brazil is where both largest (21 × 3 cm – *Prance 1825,* Pará), and smallest (8 × 1.5 cm – *Zuquim 237,* Amazonas) pinnae occur. Most specimens from Trinidad have strongly truncate pinna bases, and less costal scales and microscales. Several specimens (e.g. *Croizat 782*; *Cremers 10271*) bear a thick and resinous indusial margin, but we were not able to correlate this character with any geographical patterns or other morphological characters. *Cyclodium guianense* most resembles *C. calophyllum, C. rheophilum* (see discussion from differences), and *C. inerme*, from which it differs by the presence of conspicuous costal scales abaxially, and generally higher number of lateral pinnae (16–23 vs. 9–16 pairs). A few specimens from French Guiana show intermediate morphology between *C. guianense* and *C. rheophilum* (e.g. *Boom 1574*; *Cremers 9193*; *Granville 3093*; *Granville 14152*; *Granville 14818*). They have smaller rhizome scales and fronds, besides having narrower pinnae if compared to other specimens of *C. guianense* from the same place. All of them are associated to highly wet places, such as the margins of rivers (but other specimens also are and do not show these differences [e.g. *Granville 5301*; *Granville 8913*]). In the molecular phylogeny presented by Bohn et al. (in prep.), four accessions of *Cyclodium guianense* formed an unresolved clade with *C. rheophilum.* One of these accessions is from the Atlantic rainforest of Alagoas, Brazil (*Pietrobom 4822*), and it was previously identified as *C. heterodon* var. *abbreviatum*. Besides the phylogenetic results presented by Bohn et al. (in prep.), its narrower

pinnae and exclusively free veins support the placement of this specimen in *C. guianense*.

6. Cyclodium heterodon (Schrad.) T. Moore, Index Fil. 275. 1861. *Aspidium heterodon* Schrad., Gött. Gel. Anz. 1824: 869. 1824. *Polystichum heterodon* (Schrad.) C. Presl, Epimel. Bot. 58. 1851. *Cyrtomium heterodon* (Schrad.) T. Moore ex C. Chr., Index Filic. 197. 1905. Type: Brazil. Bahia: [Ilhéus], "in sylvis ad Almadam et in via Felisbertia", 1820, *M. Wied s.n.* (lectotype, designated by Smith, 1986: BR-0000006977009; isolectotypes: BR-0000006976941, BR-0000006976910, BR-0000006976972).

Cyclodium heterodon var. *abbreviatum* (C. Presl) A.R. Sm., Amer. Fern J. 76(2): 80. 1986. *Aspidium abbreviatum* Schrad., non Poiret (1816), Gött. gel. Anz. 1824: 869. 1824. *Polystichum abbreviatum* J. Smith, London J. Bot. 1: 199. 1842, non Lam. & DC. (1805). (To be considered a nom. nov., but illegit. because it is a later homonym). *Cyclodium abbreviatum* C. Presl, Epim. 260. 1849. nom. nov. for *Aspidium abbreviatum* Schrad. (1824). *Cyclodium abbreviatum* C. Presl Abh. Königl. Böhm. Ges. Wiss., ser. 5, 6: 620. 1851. *Nephrodium abbreviatum* (C. Presl) Fée, Mem. Foug., Gen. Fillic. 306. 1852. *Cyrtomium abbreviatum* (C. Presl) J. Sm., Ferns Brit. For. Ed. 2, 304. 1877. *Dryopteris abbreviata* (C. Presl) Kuntze, Revis. Gen. Pl. 2: 812. 1891. Type: Brazil. Bahia: "ad ripas fluv. Mucuri", 1816, *M. Wied s.n.* (lectotype, designated by Smith, 1986: BR-0000006870799; isolectotypes: BR-0000006977030, BR-0000006978686]) (Figs. 1A, 2A–D, 7H–I).

Plants terrestrial or root climber; *rhizomes* long–creeping, 0.5–1.6 cm diam., with ca. 1–4 fronds per 3 cm, scaly; *rhizome scales* basifixed, lanceolate, 0.5–2 × 0.3–1 mm, concolorous, golden to dark brown, margins entire to denticulate; *fronds* monomorphic to subdimorphic, lanceolate to elliptic; sterile fronds 42–53 × 16.5–18 cm, fertile fronds 90–99 × (34–) 40–45 cm; *petioles* stramineous, darker at base, with scales more abundant towards the base and few septate, linear, reddish–brown microscales, 21–25 cm long in sterile fronds, (39.5–) 46.5–58 cm long in fertile fronds, 3–7 mm diam.; *petiole scales* basifixed with a sinus, linear to lanceolate, 3–12 × 0.2–1.5 mm, concolorous, golden to brown, margins entire to denticulate; *laminae* 1–pinnate to 2–pinnate, subcoriaceous, with (9–) 13–21 pairs of lateral pinnae and apex gradually or subabruptly reduced and pinnatifid, 19–28 cm long in sterile fronds, (41.5–) 53.5–77 (–111.5) cm long in fertile fronds; *rachises* stramineous to tan, with an elevated center and two shallow lateral grooves abaxially and grooved adaxially, the

grooves with bacilliform, translucid, yellowish hairs, ca. 0.1 mm long, abaxially with linear, golden to brown scales, with few cells at base, ca. 1–5 mm long, also with septate, linear, brown microscales, ca. 0.5–1 mm long; *pinnae stalks* 0.5–2 cm long, with bacilliform, translucent, yellowish hairs, also with scales and microscales similar to those of the rachis; *pinnae* linear–lanceolate to elliptic, bases cuneate or truncate acroscopically and cuneate basiscopically, sometimes asymmetric at the base with an expanded auricle at the acroscopic side, apices acute to atenuate and crenate, margins undulate to crenate or pinnatifid, sterile basal pinnae 8.5–9 × 1.5–1.6 cm, fertile basal pinnae (13.5–) 16.5–23.5 × 2.3–3.6 cm, sterile medial pinnae (6–) 7.5–18 × 1.4–3 cm, fertile medial pinnae 14–16 × 1.5–3.2 cm, often with the sori distributed from the base to middle of pinna; *costae* abaxially with linear, brown scales, with few cells at base, and septate, linear, brown microscales; *laminar tissue* with microscales similar to those of the costa; *veins* anastomosed, conspicuous, 1–6 (–8) anastomoses between costa and margin, at least the basal veinlets arising from costa united; *sori* discrete, impressed, medial on veins, forming 2–6 (–8) rows of sori between costa and margin, biseriate between two main lateral veins, sometimes connivent towards costa; *indusia* peltate or sometimes with a narrow sinus, circular, ca. 0.7–1.5 mm diam, concolorous or bicolorous, stramineous to brown, with thinner, lighter, entire margins; *spores* 51.4–53.7 × 35.2–42.5 μm, the perines perforated, broadly folded and echinulated, forming anastomosing areoles, the folds high and continuous.

Distribution, ecology and conservation status.—Cyclodium heterodon is endemic to Brazil, occurring in Pará, Ceará, Pernambuco, Bahia, Espírito Santo, Minas Gerais, and Rio de Janeiro. Most of the specimens are terrestrial, having been recorded only once as epipetric (*Lopes 184*). Often associated to shaded and humid habitats within the Atlantic Rainforest, 0—950 m. The extent of occurrence (EOO) of *C. heterodon* is 524,230 km², suggested as "least concern" by GeoCAT. The area of occupancy (AOO) was estimated at 148 km², less than the threshold of 500 km² for the endangered category (EN), under the criterion B2 bii, biii. Although some specimens are often recorded in or near some protected areas of Atlantic Rainforest, most of these areas are perturbed by human activity, and therefore it is assessed as being "endangered".

EN B2bii, biii

Specimens examined. BRAZIL. Bahia: Almadina: Serra do Corcovado, 9.8 Km ao SW de Coarací na estrada para Almadina, daí N até Fazenda São José - Proprietário Senhor

Francisco, 14°42'S, 39°36'12"W, 650–750 m, 29 Jan 2005, *Matos et al. 228* (NY, MBM). Arataca: Serra do Peito de Moça, estrada que liga Arataca à Uma, ramal ca. 22.4 Km de Arataca com entrada no Assentamento Santo Antônio, RPPN "Caminho das Pedras", 15°23'30"S, 39°20'30"W, 750 m, 6 Aug 2006, *Labiak et al. 3697* (UPCB). Camacã: RPPN Serra Bonita, 9.7 km de Camacã na estrada para Jacarecí, daí 6 Km SW na estrada para a RPPN e Torre, 15°23'30"S, 39°33'55"W, 835 m, 3 Mar 2006, *Matos et al. 1095* (MBM, UPCB). Coaraci: Serra do Corcovado, próximo à propriedade do Sr. Vitorino, 14°15'35"S, 39°35'27"W, 550 m, 10 Dec 2014, *Salino et al. 16010* (BHCB). Maraú: Rod. BR 030, trecho Ubaitaba/Maraú, km 33, Folha SD 24 (14-39c), 16°25'19"S, 39°10'59"W, 5 Feb 1979, *Mori et al. 11351a* (RB). Porto Seguro: BR-5, K.18, [16°25'19"S, 39°07'48"W], 25 Aug 1961, *Duarte 6053* (UPCB). Prado: Reserva Florestal da Brasil de Holanda Industrias S.A., the entrance at Km 18 east of Itamaraju on road to Prado, 8 Km from entrance, 14°29'59"S, 39°20'W, 22 Oct 1993, *Thomas et al. 10135* (MBM). Uruçuca: Estrada de Serra Grande para Uruçuca, mata da torre do celular, área do inventário do plano de manejo do Parque Estadual Serra do Conduru, 14°29'6"S, 39°6'54"W, 380 m, 18 Jul 2005, *Matos et al. 694* (UPCB). **Ceará:** s.l., [7°20'02"S, 39°28'58"W], s.d., *Gardner 1218* (P). **Espírito Santo:** Águia Branca: Prop. Sr. Voito, 18°58'43"S, 40°44'49"W, 180–250 m, 5 Jul 2007, *Vervloet et al. 2826* (UPCB). Cariacica: Reserva Biológica Duas Bocas, localidade de Alegre, trilha do Pau Oco, 20°17'29"S, 40°31'10"W, 600 m, 18 Jan 2009, *Labiak et al. 5174* (UPCB). Conceição da Barra: Floresta Nacional do Rio Preto, 18°22'23"S, 39°50'59."W, 5– m, 10 Jun 2009, *Salino et al. 14303* (BHCB). Itaguaçu: Alto Limoeiro, 19°48'08"S, 40°50'44"W, 11 May 1946, *Brade et al. 18130* (NY, UPCB). Nova Venécia: [18°42'41"S, 40°23'33"W], 14 Nov 1953, *Duarte & Gomes 3610* (UPCB). Santa Teresa: localidade de Julião Floresta de Encosta Semidecídua, abaixo de Inselberg, 19°44'50"S, 40°32'16"W, 500 m, 10 Jul 2007, *Labiak et al. 3987* (MBM, UPCB). Sooretama: Reserva Biológica de Sooretama, floresta de tabuleiro, 19°01'21"S, 39°58'28"W, 20 m, 12 May 2008, *Heringer et al. 13342* (BHCB). **Minas Gerais:** Caratinga: Estação biológica de Caratinga, [19°43'28"S, 41°48'39"W], 7 Jul 1987, *Andrade & Costa 151* (BHCB). Jequitinhonha: Reserva Biológica da mata escura, 16°21'04"S, 40°59'58"W, 660 m, 26 Mar 2008, *Salino et al. 13168* (BHCB). Pocrane: Serra do Azeite, margens do rio Manhuaçu, 19°30'07"S, 41°38'40"W, 300 m, 01 Jun 2009, *Almeida et al. 2012* (BHCB). Santa Maria do Salto: Divisa entre Bahia e Minas Gerais, Fazenda Duas Barras, Reserva do Alto Cariri, trilha da caixa d'água, 16°24'23"S, 40°3'16"W , 950 m, 8 Feb 2006, *Matos et al. 905* (UPCB). **Pernambuco:** Jaqueira: Mata da Pedra do Cruzeiro, 08°43'21.1"S, 48°30'16"W, 600–700 m, 26 Mar 2003, *Gueiros 238* (UFP). Lagoa dos Gatos: RPPN Pedra D'Antas,

[8°41'39"S, 35°51'22"W], 12 Aug 2012, *Farias et al. 169* (UFP). São Vicente Ferrer: Complexo do Maciço do Mascarenhas, "Mata do Estado", 07°35'00"S, 35°30'00"W, 640 m, 31 Mar 1998, *Pietrobom 4207* (NY, MBM, UFP). Timbaúba: Complexo da Serra do Mascarenhas, Usina Cruangi, Engenho Água Azul, 07°37'0.6"S, 35°23'28.9"W, 304–394 m, 31 Mar 2001, *Pietrobom & Santiago 5050* (MBM, UFP). **Rio de Janeiro:** Dois Irmãos: 22°59'37"S, 43°14'15"W, Jul 1946, *Duarte 154* (RB). Santa Maria Madalena: Pedra Dubois, [21°57'13"S, 42°00'44"W], 800 m, 27 Feb 1935, *Brade 14341* (UPCB). Silva Jardim: Reserva Biológica de Poço das Antas, trilha do Morro do Calcário, ponto 850, 22°35'11"S, 42°15'00"W, 100 m, 05 Feb 1993, *Piratininga et al. 22* (MBM).

Cyclodium heterodon is characterized by monomorphic to subdimorphic sterile–fertile leaves, 1–pinnate to 1–pinnate–pinnatifid laminae, anastomosing veins (at least a few veins uniting on some pinnae), and glabrous, peltate indusia. Smith (1986) recognized two varieties for this species based on the lamina cutting and number of anastomoses: (1) var. *heterodon*, with sinuate pinnae margins and two to three pairs of united veins between costa and margin; and (2) var. *abbreviatum*, with pinnatifid pinnae margins and only one pair of united veins between costa and margin. We noticed, however, that these characters are not related to geography and there is a continuum of morphotypes between these two varieties. Our phylogenetic analysis (Bohn et al., in prep.) also shows that *C. heterodon* is monophyletic, but its varieties are still unresolved in their analysis.

It most resembles *C. meniscioides,* which overlaps in distribution with *C. heterodon* in Pará, Pernambuco, Bahia, Espírito Santo, and Minas Gerais. *Cyclodium heterodon* differs from *C. meniscioides* by its monomorphic to subdimorphic fronds (vs. strongly dimorphic), pinnatifid apex (vs. conform), less anastomoses, and entire indusia margins (vs. ciliate).

Another similar species is *C. guianense*, which occurs in Pará, and Pernambuco. *Cyclodium heterodon* differs from it by wider pinnae (1.5–3.5 vs. 1.2–2.5 cm wide) with entire to crenate apex (vs. strongly serrate apex), and anastomosing veins (vs. free veins).

Since *Cyclodium heterodon, C. meniscioides*, and *C. guianense* have a common distribution in Pernambuco, it would be likely to find some hybrids of intermediate morphology between. One probable hybrid between *C. heterodon* and *C. meniscioides* (*Lopes 628*) has the elliptic pinnae and regular anastomosing veins of *C. meniscioides* combined with

the pinnatifid pinnae margins of *C. heterodon*. Another specimen (*Lopes 184*) is possibly a hybrid between *Cyclodium heterodon* and *C. guianense*, having large, coriaceous pinnae (*C. heterodon*) and free veins (*C. guianense*). Both specimens are sterile, so no spores were seen.

7. Cyclodium inerme (Fée) A. R. Sm., Amer. Fern J. 76(2): 82, f. 11G–I. 1986. *Polystichum inerme* Fée, Mém. Foug., 5. Gen. Filic. 281. 1852. Type: French Guiana, 1850, *F. M. R. Leprieur 188* (lectotype, first–step lectotype designated by Smith, 1986: P Herbarium; **second–step lectotype, designated here**: P [00630602]; isolectotypes: P [00630603], P [00630601], MPU n.v.).

Polypodium subobliquatum Hook., Sp. Fil. 4: 240. 1862. *Nephrodium subobliquatum* (Hook.) Baker, Syn. Fil. 261. 1867. *Dryopteris subobliquata* (Hook.) Kuntze, Revis. Gen. Pl. 2: 813. 1891. *Thelypteris subobliquata* (Hook.) Ching, Bull. Fan Mem. Inst. Biol., Bot. 10: 254. 1941. Type: Surinam, s.d., *F. W. R. Hostmann 15* (lectotype, designated by Christensen, 1913: K-000590375; isolectotypes: BM-000937907, BM-000937904, P-00630604). Other syntype: Brazil. Pará: "Tanaii, ad Rio Acara, juxta Para", Sep 1849, *R. Spruce 36* (K-000590376]). (Figs. 1E, 3O–Q, 7J).

Plants terrestrial or epipetric; *rhizomes* short–creeping, 0.5–1.2 (–2) cm diam., with ca. (7–) 9–15 fronds per 3 cm, scaly at apex; *rhizome scales* basifixed, lanceate, 3–5 × 0.4–0.6 mm, concolorous, dark brown, margins entire or slightly fimbriate; *fronds* monomorphic to subdimorphic, lanceolate to elliptic, sterile fronds (33–) 44–72 (–76) × (11–) 14–25 (–29) cm, fertile fronds 50–96 × (10–) 14–28 cm; *petioles* stramineous to tan, with scales more abundant towards the base, (15.5–) 18–37 (–42) cm long in sterile fronds, (15–) 29–61 cm long in fertile fronds, (1–) 2–3 (–5) mm diam.; *petiole scales* basifixed, lanceate, (2–) 3–5 × 0.5–0.7 mm, concolorous or bicolorous, light to dark brown, sometimes with a darker center, margins slightly to strongly fimbriate; *laminae* 1–pinnate to 1–pinnate–pinnatifid, chartaceous to subcoriaceous, with 9–16 (–21) pairs of lateral pinnae and apex pinnatifid, (17.5–) 20–40 long in sterile fronds, (21–) 32–45 cm long in fertile fronds; *rachises* stramineous, rounded abaxially and grooved adaxially, the grooves with bacilliform, translucid, yellowish, hairs, ca. 0.1 mm long, abaxially with septate, linear, brown microscales, also with linear scales, ca. 0.3–1 mm long; *pinnae stalks* (0.5–) 3–7 mm long, with bacilliform, translucid, yellowish hairs, also with microscales similar to those of the rachis; *pinnae* linear to elliptic or lanceolate, bases strongly truncate acroscopically and cuneate basiscopically, asymmetric at

the base with an expanded auricle at the acroscopic side, apices acute to acuminate and crenate to serrate, margins undulate to crenate or pinnatifid, sterile basal pinnae 5–12(–16.5) × 1.7–3.5 (–4) cm, fertile basal pinnae (5.5–) 7–16.5 × 1.7–3.7 (–4.5) cm, sterile medial pinnae 6–12.5 (–14) × 1.5–3 cm, fertile medial pinnae (5.5–) 7–12 (–14.5) × 1.3–3.5 cm; *costae* abaxially with septate, linear, brown microscales; *laminar tissue* with microscales similar to those of the costa; *veins* free, conspicuous, 3–6 furcate between costa and margin, the basalmost of each segment ending just below the sinus or at the sinus; *sori* discrete, impressed, median on veins proximally to costa, terminal on veins proximally to margin, forming 4–6 rows of sori between costa and margin, biseriate between two main lateral veins; *indusia* peltate, circular, ca. 0.5–1 mm diam, concolorous, stramineous, entire or minutely ciliate margins; *spores* 51–68 × 37–46 µm, the perines non–perforated, broadly folded and echinulated, the folds high and continuous.

Distribution, ecology and conservation status.—Cyclodium inerme occurs in Amazonian Venezuela, Guyana, Suriname, French Guiana, and Brazil (Amapá, Amazonas, Pará, and north of Mato Grosso, the latter first record). This species is often recorded as terrestrial, but numerous specimens have been collected as epipetric as well. One specimen was recorded as epiphytic (*Reis 627*). Also, *C. inerme* is frequently associated to sandstone and streams, in evergreen forests, 10–1900 m. The extent of occurrence (EOO) of *C. inerme* is 2,759,584 km², recovered as “least concern” by GeoCAT. The area of occupancy (AOO) was estimated at 392 km², less than the threshold of 500 km² of the endangered category (EN), under the criterion B2 bii. As *C. inerme*, it also has a large EOO, a wide altitudinal range and occurs in several ecosystems, near or in protected areas. For these reasons, this species is assessed here as “least concern”.

LC

Specimens examined. BRAZIL. Amapá: Porto Grande: Cupixi, fazenda Boa Esperança, 0°32'N, 51°47'W, 14 Sep 2001, *Pereira & Reis 627* (BHCB). Porto de Moz: Rio Oiapoque, Igarapé Pontanarrí, [2°09'42"S, 52°55'42"W], 14 Feb 1950, *Froes 26025* (UC). **Amazonas:** Manaus-São Gabriel: Slopes and summit of Serra de Jacumim, NW of Santa Isabel, 00°25'S, 65°32'W, 100 m, 2 Jul 1979, *Poole 1822* (NY, BHCB). Médio Rio Negro: Rio Marié, local Maraúna, [1°14'56"S, 68°43'53"W], 6 Jul 1979, *Maia et al. 441* (INPA). Presidente Figueiredo: Terra-firme adjacente ao lago da Usina Hidrelétrica de Balbina, em

trilha da grade do PPBio, aproximadamente 1h e 30m de barco, 1°47'29"S, 59°17'10"W, 27 Sep 2006, *Zuquim & Jakovac 205* (INPA). São Gabriel da Cachoeira: Parque Nacional do Pico da Neblina - Trilha para o Pico da Neblina, entre o sítio Yanomami na beira da "cachoeira" e o acampamento Bebedouro velho, 0°41'54"S, 65°56'40"W, 25 Dez 2004, *Carvalho et al. 224* (INPA). **Mato Grosso:** Novo Mundo: Parque Estadual Cristalino, mata próxima a estrada, 9°35'22.0"S, 55°52'37.4"W, 342 m, 14 Jan 2009, *Henicka et al. 293* (NY). **Pará:** Ananindeua: tapaná, near Pará, [1°17'45"S, 48°24'12"W], 29 Oct 1929, *Killip 30335* (NY). Belém: Ilha de Mosqueiro, mata da Fazenda Itatuba, 01°10'56.7"S, 48°22'36.2"W, 23 Nov 2005, *Costa & Pietrobom 383* (RB). Estação Ecologia do Jari: projeto reserva genetica, SEMA, between campina and road firme, 00°75'S, 52°30'W, 13 Oct 1987, *Beck et al. 81* (NY). Parauapebas: Serra da Bocaina, 6°18'53"S, 49°53'37"W, 670 m, 13 Feb 2012, *Arruda et al. 603* (NY). Monte Alegre: Trilha para a cachoeira Chuva de Prata no Igarapé do Ambrósio, 1°26'11"S, 54°32'40"W, 302 m, 9 Dec 2015, *Almeida et al. 4176* (BHCB). **FRENCH GUIANA. Arrondissement of Cayenne:** Camopi: Montagne Cacato, SE de Cayenne, [2°20'58"N, 53°12'36"W], 17 Jan 1983, *Cremers 7828* (CAY). Gros Montagne: Mont Bakra - Région de Emérillons, 3°18'N, 52°57'W, 450 m, 17 Apr 1993, *Cremers & de Granville 13163* (CAY, UC). Matouri: Mont Grand Matoury - Ile de Cayenne, [4°52'00"N, 52°21'W], 60 m, 27 Mar 1995, *Cremers et al. 13797* (CAY). Mont Inéri: Bassin de l'Approuague, 4°22'N, 52°10'W, 300 m, 9 Sep 1997, *Cremers et al. 15364* (CAY). Montagne Plomb: 5°00'N, 52°57'W, 4 Jul 2005, *Delnatte 8* (CAY). Montsinéry-Tonnegrande: Bassin de la crique Bellevue-Nord, à 11 km au Sud de Montsinéry, le long de la piste partant vers le S-O depuis la D5, à 2,5 km à l'Ouest du pont des Cascades, 4°47'N, 52°29'W, 8 Oct 2000, *Hequet 931* (CAY). Ouanari: Route Regina - Saint Georges, D.Z. 5 - P.K. 43 - Bassin du Ba, 4°3'N, 52°1'W, 60 m, 4 Sep 1991, *Cremers & Gautier 12096* (CAY). Regina: Montagne de Kaw, environs du camp Caiman, [4°29'54"N, 52°03'27"W], 11 Jun 1979, *Cremers 5697* (CAY, UC). Roura: Route de l'Est au PK 85, piste vers Bélizon a environ 1 km de son embranchement, [4°26'04"N, 52°22'45"W], 22 Mar 1982, *Cremers 7724* (CAY). Saint-Ellie: Camp Eugène - Bassin du Sinnamary, forêt sur cuirasses latéritiques, layon R4 entre T2 e S3, 4°51'N, 53°4'W, 100 m, 7 Feb 1995, *Cremers & de Granville 13721* (CAY, UC). Sinnamary: Rivière Sinnamary à petit saut, [5°23'43"N, 52°57'47"W], 12 Feb 1979, *Cremers 5389* (CAY). **Saint-Laurent-du-Maroni:** Citron: Ascencion du massif Lucifer au depart de Citrón, [4°44'38"N, 53°56'32"W], 100 m, 9 Nov 1982, *Billiet & Jadin 1624* (CAY). Edwin: Monts Dékou-Dékou, versant est, 4°41.940', 53°55.9'W, 300–500 m, 31 May 2008, *Delnatte 1832* (CAY). Maripasoula: Gombaya Soula, bassin du Maroni, camp I, 3°37'N, 53°58'W, 125 m, 6

Jan 1989, *Cremers et al. 10135* (CAY, UC). Papaichton: Mont Kotika, versant ouest, 3°55'N, 54°12'W, 200–600 m, 9 Sep 2007, *Delnatte 1251* (CAY, UC). Saül: Layon du Grand "Circuit Boeuf Mort ", p.k. 5.4 env., forêt sur colline, [3°34'36"N, 53°10'51"W], 13 Dez 1971, *de Granville 886* (CAY). **GUYANA. Upper Demerara-Berbice:** Pubu: Arisau Mountain; Essequibo R., western peak of mountain, 05°19'N, 58°32'W, 250 m, 14 Jun 1995, *Chanderbali & Gopaul 77* (CAY). **Upper Takutu-Upper Essequibo:** Kurukuru-Baibari: Gunn's, Essequibo River, 1°39'N, 58°37'W, 240–490 m, 7 Sep 1989, *Jansen-Jacobs et al. 1507* (CAY, NY, P). **Bolívar:** Guaniamo: Hoja NB20-5, serrania Maigualida, frente 9, HP 4, quebrada que drena hacia el riachuelo y sus riberas, 6°9.3'N, 65°53.7'W, 250–350 m, 17 Apr 1989, *Stergios & Delgado 13814* (UC). **Cuyuni-Mazaruni:** Kamarang: Right bank of the Kamarang River ca. 1.5 miles above Kamarang, along trail up to 2 miles N from the river, 5°53'N, 60°40'W, 487–579 m, 16 Oct 1985, *Lellinger 2000* (CAY, US). Kokadai: Upper Mazaruni River region, vicinity of Kako, na Akawaio Indian village on the Kako River near its junction with the Mazaruni River, 5°45'N, 60°35'W, 500 m, 14 Apr 1987, *Boom & Gopaul 7296* (NY). Paruima: 1.5 km S summit of Konuktipu, [5°48'04"N, 61°03'25"W], 690 m, 22 Jul 1997, *Clarke et al. 5946* (NY). **Potaro-Siparuni:** Pakaraima Mountains: Upper Ireng R. watershed, E bank Kaatnang River at base of Achiknang, 4°59'N, 60°08'W, 700 m, 19 Jul 1994, *Henkel & Chin 5723* (CAY, INPA). Tumatumari: Base/Saddle of Eagle Montain, [5°14'06"N, 59°05'12"W], 102 m, 9 Sep 2006, *Redden et al. 4126* (CAY). **SURINAME. Brokopondo:** Brownsweg: Brownsberg Forest, [4°57'23"N, 55°10'15"W], 450 m, 1 Aug 1974, *Ingham & Ingham 33935* (NY). Kabelstation: Brownsberg Nature Park, Koemboeval, forest on laterite near waterfall, 4°56'N, 55°11'W, 400–500 m, 8 Mar 2003, *Christenhuzs & S. Bollendorff 2625* (NY). **Sipaliwini:** Amékan Tabiki: Nassau Mountains, Marowijne River, 4°48'N, 54°36'W, 400–550 m, 1 Jan 1955, *Maguire et al. 39071* (NY). Boven Coppename: Summit of tafelberg, between Lisa creek and Augustus creek, ca. 100m from western rim of the tepui, 3°55'30"N, 56°11'50"W, 575 m, 2 Jul 1998, *Evans et al. 3026* (UC). Kabalebo: Exploration of the Wilhelmina gebergte, 3°36'W-3°41'W, 56°30'N-56°34' N, 275 m, 31 Jul 1963, *Irwin et al. 54523* (NY). Tapanahony: Hab. in Montibus, qui dicuntur Nassau, in ravine along small creek near km 6.8, 4°56'33"N, 54°27'46"W, 2 Mar 1949, *Lanjouw & Linderman 2457* (US). **VENEZUELA. Amazonas:** Rio Negro: Neblina Base Camp on the rio Mawarinuma, second forested hill behind camp, 0°50'N, 66°10'W, 300–340 m, 4 a 5 Jul 1984, *Davidse & Miller 26945* (UC). Atabapo: Planicie del río Jénita, 15 km antes de desembocadura em el río Ocamo, 2°46'N, 64°52'W, 175 m, Feb 1990, *Fernandez 7234* (UC). **Bolívar:** Guanamarú: Amaruay-tepui, slope S of SW corner of tepui, 5°54'N, 62°15'W, 470–

770 m, 23 Apr 1986, *Liesner & Holst 20204* (UC). Heres: Bosques húmedos intervenidos por actividades mineras, 2 km al N-E de la margem derecha del Rio Asa, sobre coraza ferruginosa (gabro). 62 km al S-E de La Paragua, 6°16'N, 63°18'W, 370 m, 17 May 1987, *Aymard C. 6116* (UC). Poci: km 88-100 route 10 Bolivar, Sierra de Lema, 5°55'N, 61°28'W, 80–300 m, 1 Aug 1993, *Rivero & Diaz 2347-A* (UC). Roscio: Zona minera "Supamo-Parapoy", en Parapapoy, 06°35'N, 62°40'W, 450 m, 1993, *Diaz & Nico 1320* (UC). Sección Capital Sifontes: A lo largo de la quebrada Acarabisi, límites del Estado Bolívar com la zona de reclamación, [6°56'26"N, 60°27'25"W], 3 Feb 1982, *Aymard et al. 954* (UC).

The protologue of *Polystichum inerme* Fée (1852) cited the following information: “Habitat in Guyanâ gallicâ (Leprieur, n. 188, Herb. clar. Mougeot.)”. According to Stafleu & Cowan (1976), the Mougeot Herbarium is now at MPU. This specimen was not located by Smith (1986), who cited an “isotype” at P. We also did not find this specimen at MPU, so we are here designating a lectotype at P. There are two other duplicates of *Leprieur 188* at P, and these are here considered isolectotypes.

Cyclodium inerme is characterized by its short, crenate to pinnatifid pinnae, free veins, and lack of conspicuous scales on costae. It mostly resembles *C. alansmithii* (which see for differences). Another similar species is *C. guianense* (see for differences), which has a wider distribution, but overlaps in nearly all locations, excluding Colombia, Bolivia, and some states of Brazil. Furthermore, *C. inerme* seems to be more frequent in Guyana and Venezuela than *C. guianense*.

Cyclodium inerme is relatively uniform in morphology across its distribution. Both crenate to deeply pinnatifid fronds occur in all localities, but more dissected laminae seem to be more common in Brazil, and specimens from Suriname often have shorter pinnae. The results presented by Bohn et al. (in prep.), shows that *C. inerme* is sister to *C. alansmithii*. The absence of scales on costae abaxially is a synapomorphy to this clade.

Four specimens with the same collector’s number (8913) and with the same label, are probably mixed. Two of them refer to *C. inerme* (*Granville 8913*, INPA; *Cremers 8913*, UC), whereas the other two refer to *C. guianense* (*Granville 8913*, NY; *Cremers 8913*, CAY). Another collection (*Cremers 12096*) has two parts that belong to *C. inerme* (CAY 52160 and CAY 52161) and another that is a fertile frond of *C. meniscioides* (CAY 52162). Lastly, one collection from CAY (*Cremers 10180*) refers to *C. guianense* (CAY 018483), and from UC refers to *C. inerme* (UC 1556093).

8. Cyclodium meniscioides (Willd.) C. Presl, Tent. Pterid. 85. 1836. *Aspidium meniscioides* Willd., Sp. Pl. 5: 218. 1810. *Nephrodium meniscioides* (Willd.) J. Sm., J. Bot. (Hooker) 4: 188. 1841. *Dryopteris meniscioides* (Willd.) Kuntze, Revis. Gen. Pl. 2: 813. 1891. *Stigmatopteris meniscioides* (Willd.) K. U. Kramer, Proc. Kon. Ned. Akad. Wetensch., C 71: 521. 1968. Type: Brazil, s.d., *J. C. von Hoffmannsegg s.*n (holotype: B-W19737-010]).

Aspidium confertum Kaulf., Enum. Filic. 232. 1824. *Cyclodium confertum* (Kaulf.) C. Presl, Tent. Pterid. 85. 1836. *Nephrodium confertum* (Kaulf.) J. Sm., Hooker's J. Bot. Kew Gard. Misc. 4: 188. 1841. "*Cyrtomium" confertum* Presl ex C. Chr., Index Filic. 197. 1905 [an error by Christensen for *Cyclodium confertum*]. *Dryopteris meniscioides* var. *conferta* (Kaulf.) C.V. Morton, Bull. Torrey Bot. Club, 66(1): 51. 1939. Type: French Guiana ["Cayenna"], *L. C. Richard s.n.* (**lectotype, here designated**: P-00630615; isolectotypes: P-00630616, P-00630617, P-00630618, P-00630619; probable isolectotypes: LE n.v.).

Aspidium hookeri Klotzsch, Linnaea 20: 364. 1847, nom. illeg. hom., non *A. hookeri* Sweet, Hort. Brit. (ed. 2) 579. 1830.

Campium molle Copel., Philipp. J. Sci. 37: 390, f. 41, t. 29. 1928. *Bolbitis mollis* (Copel.) Ching in C. Chr., Index Filic., Suppl. 3: 49. 1934. Type: Brazil ["Ceylon"], s.d., *G. Gardner s.n.* (holotype: K-000590377). See Hennipman (1977, page 314) for discussion.

Cyclodium meniscioides (Willd.) C. Presl var. *paludosum* (C. V. Morton) A. R. Sm., Amer. Fern J. 76(2): 87. 1986. *Dryopteris paludosa* C. V. Morton, Bull. Torrey Bot. Club 66(1): 50. 1939. *Stigmatopteris paludosa* (C. V. Morton) R. M. Tryon & A. F. Tryon, Rhodora 83(833): 136. 1981. Type: Colombia, Dept. Antioquia, Puerto Berrio, 130–140 m, 11–13 Jan 1918, *F. W. Pennell 3723* (holotype: NY-00149458; isotype: US-00067164).

Cyclodium meniscioides (Willd.) C. Presl var. *rigidissimum* (C. Chr.) A. R. Sm., Amer. Fern J. 76(2): 87. 1986. *Cyclodium rigidissimum* C. Chr., Bot. Tidsskr. 25: 79–80. 1903. *Aspidium rigidissimum* C. Chr., Bot. Tidsskr., 25: 79–80. 1903, nom. inval., as synonym of *C. rigidissimum* C. Chr. Type: Guyana ("Brazil"), *C. F. Appun* ("*A. F. M. Glaziou*") *12374* [according to Smith (1986), the syntypes were actually collected in Guyana by Appun and later distributed by Glaziou under his number; *Appun 1176*, housed at K, may be part of the same gathering] (**lectotype, here designated**: C-10020678; isolectotypes: B-200040062, B-200040063, C-10020676, C-10020677, G [3 sheets] n.v., P-00630614, cited by Smith, 1986]) (Figs. 1F, 2E–H, 7K–L, 8A).

Plants terrestrial or root climber; *rhizomes* short to long–creeping, 0.5–1.5 cm diam., with ca. 3–5 (–8) fronds per 3 cm, scaly; *rhizome scales* basifixed, lanceate, 4–15 × 0.4–1 mm, concolorous, light to dark brown, margins dentate to fimbriate, *fronds* subdimorphic to dimorphic, lanceate to lanceolate; sterile fronds (34–) 46.5–137 (–150) × (14–) 26–40 cm, fertile fronds (68–) 75–150 (–184) × (6.5–) 14–27 cm; *petioles* stramineous to dark brown, with several scales more abundant towards the base and sometimes with linear, septate, dark brown microscales, 22.5–38 cm long in sterile fronds, (28–) 46.5–77.5 (–120.5) cm long in fertile fronds, 2–6 (–10) mm diam.; *petiole scales* basifixed with a narrow sinus, lanceate, 3–12 × 0.2–3 mm, concolorous, light to dark brown, margins dentate to fimbriate; *laminae* rarely simple to 1–pinnate, subcoriaceous to coeiaceous, with (1–) 3–8 (–13) pairs of lateral pinnae, often with a reduced pinna before the apical and conform apex; 29–47 cm long in sterile fronds, (21.5–) 32.5–80 cm long in fertile fronds; *rachises* stramineous to tan, grooved adaxially, grooves with bacilliform, translucid, yellowish hairs, ca. 0.1–0.2 mm long, and sometimes with linear, septate, light to dark brown microscales, ca. 0.3–0.4 mm long, abaxially with microscales and hairs similar to those of the grooves, also sometimes with scales composed of few cells at base, ca. 2 mm long; *pinnae stalks* 2–4 (–6) mm long, with hairs, microscales and sometimes scales similar to those of the rachis; *pinnae* lanceate to lanceolate, sometimes ovate, bases cuneate or truncate, sometimes slightly asymmetric, truncate and larger acroscopically, cuneate basiscopically, apices acute to acuminate, margins entire to crenate, the fertile more dissected, sterile basal pinnae 1.2–25 × 3.5–7 cm, fertile basal pinnae 7–17 (–26) × (0.7–) 1.5–3.5 (–8.5) cm, sterile medial pinnae 11.5–19 × 3.5–6.5 cm, fertile medial pinnae (5–) 11.5–15.5 × 1–3.5 cm; *costae* abaxially with linear, septate, dark brown microscales, and light to dark brown scales, composed of few cells at base, ca. 1 mm long; *laminar tissue* with scales and microscales similar to those of costa; *veins* anastomosed, inconspicuous, with 4–7 areoles between costa and margin, sometimes from the united veinlets there is a free tip, or the tip is united to the next veinlets; *sori* discrete, impressed, medial on veins, forming 4–7 rows of sori between costa and margin, biseriate between two main lateral veins, frequently confluent at maturity with the two basal ones united; *indusia* peltate, circular, ca. 1–1.5 mm diam, concolorous, light to dark brown, the margins entire, or minutely to densely ciliate; *spores* 53–63 × 36–47 μm, the perines perforated, broadly folded and densely echinulated, forming anastomoses areoles, the folds high and continuous.

Distribution, ecology and conservation status— Cyclodium meniscioides has the widest distribution of *Cyclodium*, occurring from Colombia to Paraguay and NE Argentina, Trinidad, Venezuela, Guyana, Suriname, French Guiana, and nearly all over Brazil. This species is often recorded as terrestrial or climbing on tree trunks up to 1 to 2 m high. Also, some specimens are cited as epiphytes (e.g. *Tillett 44945; Morales 1205; Granville 2894; Prance 15945; Croat 18579*) or epipetric (*Cremers 10851; Granville 15488; Delnatte 722*). In general, *C. meniscioides* occurs in humid and shaded forests, 0–1250 m. The extent of occurrence (EOO) of *C. meniscioides* is 12,226,986 km², recovered as "least concern" by GeoCat. The area of occupancy (AOO) was estimated at 852 km², less than the threshold of 2,000 km² of the vulnerable category (VU). This species is the most widely distributed in the genus, has a large EOO, a wide altitudinal range and occurs in many different ecosystems. Because of that, it is more likely that its area of occupancy should trespass the threshold of any threatened category. *Cyclodium meniscioides* is assessed here as "least concern".
LC

Specimens examined. ARGENTINA. Corrientes: Ituzaingó: Desembocadura del Ayo, garapé em el Rio Paraná, 45 km al E de Ituzaingó, [27°34'58"S, 56°46'53"W], 24 Apr 1975, *Schinini et al. 11245* (MBM). **BOLIVIA. Beni:** Santa Cruz: Luisita, [13°04'59"S, 67°15'W], 180 m, 03 May 1984, *Beck 10214* (LPB). Vaca Diez: Province of Vaca Diez, 3.3 km from the road between Riberalta and Guayaramerín, on the old road to Cachuela Esperanza, ca. 18 km E of Riberalta, 11°05'S, 65°50'W, 230 m, 9 Sep 1981, *Solomon 6186* (BT, NY, UC). **La Paz:** Iturralde: San José de Uchupiamonas, [14°12'59"S, 68°04'59"W], 550 m, s.d., *Williams 1202* (NY). **Pando:** Abuna: al norte del rio Orton Barraca, San Juan de Nuevo Mundo, campamento 18, hasta Democracia, a 18 km al norte de la barraca, [10°45'59"S, 66°43'59"W], 170 m, 07 Jun 1992, *Vargas 655* (LPB). Manuripi: ca. 20 km. South of Rio Manuripi on the road to Chivé, 11°58'S, 68°35'W, 12 Aug 1982, *Sperling & King 6596* (LPB, NY, UC, US). Nicolás Suárez: camino Cobija-Puerto Rico, comunidad Santa Elena, entrando por un camino a 4 km de esta localidad, en dirección a Cobija, [11°03'59", 67°51'59"W], 220 m, 08 Feb 2003, *Jiménez 1987* (LPB). **Santa Cruz:** Velasco: Parque Nacional Noel Kempff M., campamento La Torre, 13°39'20"S, 60°49'08"W, 200 m, 21 Nov 1993, *Arroyo & Gutierrez 377* (NY, BX). **BRAZIL. Acre:** Cruzeiro do Sul: Japiim, Igapó de Brasília, 7°37'34"S, 72°48'16"W, 26 Jul 1972, *Francisca & Marquete 676* (RB). Mâncio Lima: PARNA Serra do Divisor, trilha para a Cachoeira do Ar Condicionado, 07°27'13.4"S, 73°41'30.7"W, 240 m, 23 Aug 2008, *Fiaschi et al. 3383* (RB). **Alagoas:**

Ibateguara: Engenho Coimbra, Grota do Varjão, 09°00'12.4"S, 35°51'55.9"W, 380–400 m, 19 Dec 2000, *Pietrobom & Santiago 4719* (UFP). Murici e Messias: Estação Ecológica de Murici, 09°16'48"S, 35°45'20"W, 100–650 m, 7 May 2009, *Pereira & Silva 1121* (UFP). **Amapá:** Porto Grande: Horto do IEPA, 0°42'N, 51°28'W, 27 Aug 2001, *Pereira et al. 572* (BHCB). **Amazonas:** Manaus: ca. 90 km. N de Manaus, Distrito Agropecuário da SUFRAMA, Rodovia BR 174, km 64, depois 7 km leste na ZF3, Fazendo Porto Alegre, 02°22'S, 59°57'W, 50–125 m, 21 May 1992, *Nee 42791* (INPA, MBM, NY). Maraã: Rio Japurá, environs of town of Maraã, Headwaters of lago Maraã, 1°47'S, 65°37'W, 7 Dec 1982, *Plowman et al. 12309* (INPA). Santa Isabel do Rio Negro: Parque nacional do pico da Neblina - Trilha para a cachoeira do Anta, entre o acampamento e Cuiabixi e Mao, subindo a Serra da Neblina, 0°00'S, 65°00'W, 1250 m, 28 Dec 2004, *Carvalho et al. 261* (INPA). Santo Antônio do Içá: Santo Antonio de, Unidade de conservação federal Javari-Buriti. Flooded region abutted by the Amazon river to the north and two small blackwater canals to the west and east, [3°07'34"S, 67°49'36"W], 60 m, 15 Jun 2013, *Householder & Moreira 2935* (INPA). São Gabriel da Cachoeira: Road margins Camanaus-Uaupés road, near Camanaus, [0°06'17"S, 66°54'37"W], 1 Nov 1971, *Prance et al. 15945* (INPA). **Bahia:** Arataca: Serra das Lontras, ca. De 7 km no ramal que liga o povoado de Itatinguí à Serra das Lontras, 15°12'10"S, 39°24'29"W, 600 m, 12 Feb 2005, *Matos et al. 406* (UPCB). Camacan: RPPN Serra Bonita, 10 km W de Camacan na estrada para Jacarecí, 6 Km SW na estrada para a RPPN e Torre de transmissão, 15°23'35"S, 39°33'53"W, 850 m, 11 Aug 2006, *Labiak et al. 3706* (UPCB). Ilhéus: Litoral Sul, assentamento Bom Gosto, 14°41'S, 39°07'W, 23 Jun 2001, *Guedes et al. 9390* (MBM). Santa Teresinha: 14,5 km da rod. Elísio Medrado/Sta. Teresinha, Torre da Embratel, ca. 7 km do Distr. De Pedra Branca, Serra da Jibóia, 12°51'13"S, 39°28'33"W, 750 m, 24 Feb 2000, *Jardim et al. 2853* (MBM, NY). **Ceará:** Maranguape: Serra do Maranguape, [3°54'51"S, 38°43'02"W], 27 Jun 1981, *Nunes & Martins 18* (UFP). **Espírito Santo:** Linhares: Reserva Florestal de Linhares, Aceiro Ceolin, 19°09'40.4"S, 40°04'16.4"W, 30–60 m, 12 Feb 2007, *Almeida et al. 708* (BHCB). Santa Teresa: Alto de Santo Antonio, terreno do Bozza, 19°54'31"S, 40°35'28"W, 760 m, 12 Jul 2007, *Labiak et al. 4059* (UPCB). **Goiás:** Aporé: Rio Correntes, 18°57'55"S, 51°55'35"W, 2 Aug. 1995, *Pietrobom 2367* (MBM). Caçu: Fazenda Boa Vista da Felicidade, 18°33'24"S, 51°07'51"W, 300–400 m, 13 Nov 1994, *Pietrobom 1484* (MBM). Goiânia: [16°40'54"S, 49°15'43"W], Dec 1936, *Brade 15360* (RB). Goiatuba: Rod. GO-211, próximo de Venda Seca, 18°00'45"S, 49°21'17"W, 24 Jan 1996, *Pietrobom 2721* (MBM). Jataí: Queixada, 17°52'53"S, 51°42'52"W, 11 Apr. 1959, *Macedo 1839* (MBM). Marzagão: Rod. GO-413, ca. 2km do rio

Bajé, 17°58'53"S, 48°38'25"W, 23 Jan 1996, *Pietrobom 2658* (MBM). Portelândia: Vereda com buritizal, 17°22'S, 52°39'W, 850 m, 5 Jul 1996, *Windisch 8148* (BHCB). Quirinópolis: Rod. GO-206, ca. De 4 km de Quirinópolis, próximo da rodovia, 18°26'54"S, 50°27'06"W, 24 Jan 1996, *Pietrobom 2743* (MBM). **Mato Grosso:** Alta Floresta: ca. 12 km da cidade de Alta Floresta, 10°S, 56°W, 5 May 1986, *Windisch 4743* (UC). Barra do Garças: 256 km along new road NNE of village of Xavantina, at Royal Society-Royal Geographic Society Base Camp, area of 10 km radius around Base Camp is situated on crest of the Serra do Roncador, a gently-sloped divided between Xingu drainage (via Rio Suiá Miçu), 12°51'S, 51°45'W, 450 m, 9 Sep 1968, *Eiten & Eiten 8639* (NY). Chapada dos Guimarães: Parque Nacional da Chapada dos Guimarães, caminho para as cabeceiras do rio, 15°18'48"S, 55°30'22"W, 286 m, 1 Mar 2011, *Almeida et al. 2665* (BHCB). Colíder: Resgate de Flora da UHE Colíder, lote B estrada para supressão, floresta do "Planalto dos Parecís, 10°57'02"S, 55°34'10"W, 272 m, 17 Mar 2015, *Lautert et al. 489* (MBM). Nova Canaã do Norte: Resgate de FLORA da UHE Colíder, lote A de supressão, floresta do "Planalto dos Parecís", 10°58'09"S, 55°41'26"W, 274 m, 25 May 2015, *Engels et al. 3539* (MBM). Rondonópolis: Rod. BR-163, Rio Poxoreu, [16°28'24"S, 54°37'56"W], 12 Nov 1975, *Hatschbach 37462* (MBM). Santo Antônio do Leverger: 2 km de São Vicente, estr. Velha de São Lourenço, antiga cabeceira, [15°51'49"S, 56°05'01"W], 30 Nov 1990, *Windisch et al. 5749* (RB). Vera: ca. 4 km da BR 163, 12°19'27"S, 55°18'56"W, 6 Oct 1997, *Windisch 8843* (BHCB). Vila Bela da Santíssima Trindade: Parque estadual serra de Ricardo Franco, mata de galeria do Córrego Cascata, cachoeira dos Namorados, 14°56'20"S, 60°01'33"W, 301 m, 6 Mar 2011, *Almeida et al. 2749* (BHCB). **Mato Grosso do Sul:** Jatei: Parque Estadual das Várzeas do rio Ivinhema, [22°55'07"S, 53°39'12"W], 6 Sep 2003, *Clemente et al. 122* (UPCB). Ponta Porã: Fazenda, [22°32'27"S, 55°42'43"W], s.d., *Carneiro 64* (BHCB). **Minas Gerais:** Araguari: distrito de Paracaíba, fazenda mata da água fria, 18°29'49.6"S, 48°24'16"W, 860 m, 27 Jan 2007, *Salino et al. 11542* (BHCB). Catuji: BR-116, Teófilo Otoni em direção a Catuji, margem esquerda da estrada, 17°24'22"S, 41°30'56"W, 7 Jan 2011, *Paula et al. 74* (UPCB). Santa Maria do Salto: Divisa entre Bahia e Minas Gerais, fazenda Duas Barras, Reserva do Alto Cariri, trilha da caixa d'água, 16°24'23"S, 40°3'16"W, 950 m, 8 Feb 2006, *Matos et al. 924* (MBM, UPCB). **Pará:** Belém: Ilha de Mosqueiro, mata do Pirajuçara, 01°10'38.9"S, 48°22'08"W, 8 Aug 2005, *Costa 271* (RB). Itaituba: Estrada Santarém-Cuiabá, BR 163, km 794, Serra do Cachimbo, ± 7km dentro da mata, [5°26'03"S, 56°35'29"W], 23 Apr 1983, *Amaral et al. 922* (INPA). Monte Alegre: Área de reserva da Pousada Vale do Paraíso, trilha entre a sede da pousada e a cachoeira Preciosa, na área da cachoeira, 1°29'17"S, 54°30'W, 121 m, 12 Feb

2018, *Almeida et al. 4743* (BHCB). Parauapebas: Serra sul, corpo C, 6°24'01"S, 50°23'18"W, 700 m, 18 Mar 2009, *Viana et al. 4137* (BHCB). **Pernambuco:** Bonito: Estrada para a Colônia, Reserva Biológica Municipal, região com formação de colinas e vales em forma de "V", 8°31'10"S, 35°43'33"W, 05 May 1998, *Pietrobom 4297* (MBM). Igarassu: Refúgio Ecológico Charles Darwin, 07°49'27"S, 34°56'52"W, 18 Feb 1999, *Santiago 18* (UFP). Jaqueira: Mata do Fervedouro, 08°42'37"S, 35°50'01"W, 600–700 m, 27 Mar 2003, *Gueiros 180* (UFP). Lagoa dos Gatos: RPPN Pedra D'Antas, [8°41'39"S, 35°51'22"W], 14 Oct 2012, *Farias et al. 94* (UFP). São Vicente Ferrer: Complexo da Serra do Mascarenhas, "Mata do Estado", 07°35'00"S, 35°30'00"W, 600–650 m, 17 Aug 1998, *Pietrobom 4395* (UFP, MBM). Timbaúba: Complexo da Serra do Mascarenhas, Usina Cruangi, Engenho Água Azul, área do poço caudaloso, 07°36'47.5"S, 35°23'26.7"W, 304–394 m, 30 Jan 2001, *Pietrobom & Santiago 4761* (UFP, MBM). **Piauí:** Santa Filomena: 9°39'54"S, 45°47'32"W, 14 May 2013, *Santos et al. 337* (MBM). **Rondônia:** Pimenta Bueno: Parque municipal de Pimenta Bueno, 11°40'21"S, 61°11'37"W, 180 m, 1 Dec 2006, *da Costa 19* (UPCB). Porto Velho: Estação Ecológica Cuniã (ESECC), Grade PPBio, LO2-2800, 8S°03'45"S, 63°28'45"W, 24 5 2013, *Cabral & Sampaio 30* (UNIR). Vilhena: Local alagável, temporariamente seca, ponto 1201, 13°00'51"S, 60°22'02"W, 6 Dec 2013, *Bigio et al. 1201* (RB, UNIR). **São Paulo:** Casa Branca: Rodovia (SP-215) BR-267 Casa Branca/Várzea Grande do Sul, ca. 2 km da cidade, 21°46'S, 47°04'W, 650 m, 17 Jul 1995, *Pietrobom 2013* (MBM). Itirapina: Estação Ecológica de Itirapina, 22°14'S, 47°56'W, 705 m, 12 Mar 2002, *Dittrich et al. 1096* (MBM). Patrocínio Paulista: Reserva de Carrado da UFSCar, 20°45'59"S, 47°14'55"W, 15 Feb 2013, *Canestraro & Matos 537* (MBM). **Tocantins:** Palmas: Fazenda Mundial, [10°15'56"S, 48°19'49"W], 10 Jan 2006, *Sobral & Larocca 10365* (BHCB). Ponte Alta do Tocantins: Cachoeira da Fumaça, Jalapão, [11°09'20"S, 47°00'40"W], 27 May 2008, *Cordeiro et al. 2717* (MBM).

COLOMBIA. Amazonas: La Chorrera: Gran Resguardo Prédio Putumayo, Asociación Indígena (ASICACH), Cabildo Capitanía, San Isidro, rio Igara-Parana, 1°24'56.51"S, 72°45'52.6"W, 161 m, 26 Aug 2015, *Rodríguez et al. 8572* (HUA). La Pedrera: Comisaría del Amazonas, lado oeste del Cerro de Cupatí (Cerro de la Pedrera), cerca de la Pedrera, lado norte del Río Caquetá, 1°16'S, 69°36'W, 325–390 m, 8 Mar 1990, *Churchill et al. 16039* (HUA). Leticia: 7 km North of Leticia near road, [4°10'07"S, 69°56'27"W], 8 Feb 1969, *Plowman 2452* (NY). Puerto Arica: Rio Igara-Parana (affl. Rio Putumayo), corr. La Chorrera, occidente (Bella Vista) piste menant au fleuve, bord du fleuve, [2°08'14"S, 71°59'32"W], 29 May 1974, *Sastre 3017* (P). **Caquetá:** La Montañita, vereda Itarca, Reserva natural Itarca, quebrada Las Lajas, 1°32'42.1"N, 75°28'02.2"W, 350 m, 31 Oct 2010, *Rodríguez et al. 7115*

(NY). **Putumayo:** Orito: resguardo indígena Cañaveral Miraflores, finca Alto Bonito La Esperanza, 0°44'42.4"N, 76°48'27.7"W, 408 m, 21 Nov 2013, *Rodríguez et al. 8075* (NY). Puerto Leguízamo: Comisaría del Putumayo, selva higrófila del río Putumayo em Puerto Ospina, [0°08'19"N, 75°51'19"W], 230 m, 14 Nov 1940, *Cuatrecasas 10563* (US). **Vaupés:** Carurú: Medio Caqueta entre los raudales El Tijereto y El Quinché, 1°1'19"N, 71°33'7"W, 14 Mar 2001, *Benavides et al. 640* (HUA). **ECUADOR. Morona-Santiago:** Limon Indanza, Región de la Cordillera del Condor, cuenca del Río Coangos, Comunidad Shuar de Kuankus, sendero que conduce hacia la comunidad Yunkumas, 3°02'36"S, 78°13'03"W, 850 m, 14 Jun 2005, *Morales & Tupiza 1205* (UC). Logroño: Región de la Cordillera de Cutucú, Centro Shuar Tumpaim, cordillera de Saunto y Satap., 02°41'05"N, 77°55'14"W, 540 m, 11 Dec 2003, *Toasa et al. 9400* (UC). Taisha Canton: El centro Shuar Kankaim! (Cangaime) y alredadores, 6 horas a pie al oeste del Taisha, cerca el Rio Kankaim!, [2°20'43"S, 77°0030'55"W], 16 Sep 1985, *Baker et al. 6381* (NY). **Pastaza:** Chichirata: Oil exploration camp Chichirota, on the Río Bobonaza, 2°22'S, 76°40'W, 30 m, 26 Jul 1980, *Ollgaard et al. 35360* (NY, UC, US). **FRENCH GUIANA. Arrondissement of Cayenne:** Arataï: Camp Arataï on Arataye River, a short distance from the mouth of the Arataye River at junction with the Approuague River, layon Montagne Kwata, 3°59'N, 52°34'W, below 200 m, 7 Nov 2003, *Mori et al. 25659* (NY). Camopi: Mont Saint-Marcel, zone sud-est du massif, petite crique à l'est du sommet central, 2°23'00"N, 53°00'20"W, 380 m, 25 Jul 2002, *de Granville et al. 15488* (CAY). Cayenne: Petit Montagne Tortue-Tibourok, along trail from Corbet to waterfall, [4°55'18"N, 52°19'01"W], 16 Mar 2010, *van der Werff 23484* (UC). Montsinéry-Tonnegrande: Ancien bagne des Annamites, région de Cayenne 2, bord du Bagne des Annamites, à 8km au sud de Montsinéry, 4°49'N, 52°30'W, 10 m, 8 Mar 1997, *Boudrie 2836* (CAY). Ouanary: Route Régina - Saint Georges D.Z. 5 - P.K. 43 - Bassin du Ba, 4°3'N, 52°1'W, 20 m, 6 Apr 1991, *Cremers & Gautier 11983* (CAY, US). Regina: Mont Chauve, 3°49'N, 52°44'W, 100 m, 16 Apr 1997, *Cremers & Crozier 15020* (CAY). Remire-Montjoly: Environs de Cayenne, [4°51'42"N, 52°17'49"W], 1836, *Mille s.n.* (P). Roura: Camp Caïman - ASARCO - Montagne de Kaw, 4°32'N, 52°13'W, 10 m, 12 Mar 2004, *Bordenave & Betian 7927* (CAY). Saint-Elie: Station des Nouragues - Bassin de l'Approuague - arataye berge des cascades, 4°3'N, 52°42'W, 90 m, 19 Nov 1989, *Cremers 10851* (UC). Saint-Georges: Savane Roche du Quatorze Juillet - Bassin du Bas-oyapock, 3°58'N, 51°52'W, 50 m, 19 Apr 1991, *Cremers 12313* (CAY). **Saint-Laurent-du-Maroni:** Sinnamary: Saut Parasol - Bassin du Sinnamary, 02°30'53"N, 51°20'04"W, 2 Jun 2009, *Gonzalez 1752* (CAY). Élysée: Collines et criques situées à l'ouest de la vallée de la crique Elysée et de la piste allant d'Elysée à

Emmanuel, à 9,5 km à l'WNW de Citron, à 80 km au sud de Saint-Laurent- du-Maroni, 4°45'N, 54°2'W, 100 m, 13 Jul 1999, *Boudrie 3212* (CAY). Mana: Crique Jean-Pierre - Bassin de l'Approuague, 4°17'N, 52°12'W, 30 m, 7 Dec 1994, *Cremers et al. 13573* (CAY). Maripasoula: Gombaya Soula - Bassin du Maroni. Camp I, 3°37'N, 53°58'W, 125 m, 6 Jan 1989, *Cremers et al. 10135* (CAY). Saül: Tropical moist forest. Monts La Fumée, 3°37'N, 53°12'W, 200–400 m, 7 Oct 1982, *Boom & Mori 1894* (NY). Sparouine: Piste minière Coralie (RN2) - ASARCO 5: zone Crique Lalanne, Camp no. 2 P.K. 6, entre les points P-49 et P-50, 4°30'16"N, 52°17'00"W, 20 m, 18 May 2004, *de Granville & Bordenave 16207* (CAY). **GUYANA. Barima-Waini:** Baramanni: Northwest district, 7°45'N, 59°5'W, 18-28 Sep 1923, *de la Cruz 4302* (UC). Morawhanna: Waini river, northwest district, 8°20'N, 59°40'W, Apr 1923, *de la Cruz 3844* (UC). Port Kaituma: ± 5 km SW of Sebai Village, village on Sebai River, tributary of Kaituma R., 7°49'N, 59°57'W, 15–20 m, 16 Dec 1991, *Hoffman et al. 610* (CAY). **Cuyuni-Mazaruni:** Isseneru Village: Upper Mazaruni River Basin, NE side, [6°22'56"N, 60°22'39"W], 800 m, 28 Jul 1960, *Tillett et al. 44945* (NY). Kamuda Village: Pakaraima Mts. Imbaimadai Karowrieng River above Maipuri Falls, 5°41'15.2"N, 60°12'54.6"W, 576 m, 25 Jan 2004, *Redden et al. 1527* (NY). Karrau: Penal Settlement, [6°24'21"N, 58°40'10"W], Dec 1919, *Hitchcock 17124* (NY). Tulameng Mountain: eastern slope, 5°33'28.3"N, 60°57'53.8"W, 976–990 m, 18 Jul 2010, *Redden et al. 7014* (CAY). Paruima: 9 km W, 0.2-0.5 km E of Ararata scrub area, 5°49'N, 61°08'W, 780 m, 5 Jul 1997, *Clarke et al. 5383* (US). **Demerara-Mahaica:** Hyde Park: Heliconia farm of B. Ramsaroop. 1.5 km from Soesdyk on Linden Highway, then 1 km S, 06°32'N, 58°13'W, 10–15 m, 18 Oct 1992, *Kellof et al. 860* (CAY, NY). **Essequibo Isl-W Demerara:** Santa Mission: Arawak Amerindian land, Timberhead Resort, 3 km up Pokerero R from Santa Mission, N of compound, 06°35'N, 58°21'W, 5–15 m, 28 Jan 1992, *Hoffman & Patterson 887* (CAY). **Pomeroon-Supenaam:** Issoroso: Pomeroon R. watershed; Issororo River, 10-12 km W of confl. with Pomeroon River, near Mango Landign, 7°14'N, 58°58'W, 5–15 m, 17 Sep 1992, *Hoffman & Roberts 2678* (CAY). **Potaro-Siparuni:** Post: Iwokrama Rain Forest Reserve, karupukari, 3 mi SW on Karupukari/Annai Road, 04°37'N, 58°43'W, 70 m, 17 Mar 1997, *Mori et al. 24395* (NY). Wiapri: Pakaraima Mts, Mt. Wokomung, Suruwabaru Creek, 2-3 km upstream from its juncture with Yuarka R., 5°03'N, 59°53'W, 675–750 m, 10 Feb 1993, *Henkel et al. 1244* (CAY). **Upper Demerara-Berbice:** Pubu: 5°20'N, 58°40'W, 150–200 m, 5 Jun 1986, *Pipoly 7552* (US). **Upper Takutu-Upper Essequibo:** Makarapan Mountain: along Makarapan Creek, 3°59'N, 58°57'W, 250 m, 18 Sep 1988, *Maas et al. 7527* (CAY). Shea: Bushmouth Shea to Quitari R., 2°54'N, 59°7'W, 200 m, 29 Aug 1995, *Jansen-Jacobs et*

al. 4924 (CAY, UC). **PARAGUAY. Caaguazú:** Caaguazú: In viciniis Caaguazú, [25°27'38"S, 56°03'34"W], 1905, *Hassler 9049* (NY, UC). **Paraguarí:** Sapucai: Prope Sapucay, [25°41'11"S, 56°57'40"W], 23 Sep 1919, *Hassler 12969* (P). **Upper Pananá:** In regione fluminis Alto Paraná, [25°11'33"S, 54°32'39"W], 1909-10, *Fiebrig 63* (US). **PERU. Amazonas:** Aramango: 5°14'40"S, 78°21'24"W, 430m , 8 Mar 1998, *van der Werff et al. 14538* (NY, UC). Bagua: Distrito Imaza, comunidad Aguaruna Putuim, anexo de Yamayakat, 240 degres SW de Putuim (285 degrees SW de Yamaykat), [5°12'01"S, 78°21'52"W], 700–750 m, 20 Jan 1996, *Díaz et al. 7722A* (UC). Chávez Valdivia: Primary forest near yuwi inci creek, 6 h walk from the Pongo Mori, Rio Comain, trail to Kusu (Rio Numpatakai), [4°27'S, 78°13'00"W], 518–610ft m, 11 Mar 1973, *Berlin 949* (UC). Condorcanqui: Bajo Cachiaco, Tayuntsa, Quebrada Japaim, río Nieva, [4°20'22"S, 77°43'07"W], 15 Aug 1997, *Albánc et al. 10016* (UC). Santa María de Nieva: Above Pongo de Manseriche, streamlet near mouth of Rio Santiago, [4°37'27"S, 77°52'54"W], 210 m, 1 Dec 1931, *Mexia 6193a* (UC, US). **Loreto:** Aguaytia: Primary forest on steep slopes along Rio Aguaytia, [9°02'06"S, 75°30'22"W], 3 Oct 1972, *Croat 20967* (UC). Llanchama: San Juan Bautista, vicinity of Lago Llanchama near Río Nanay, [3°50'41"S, 73°24'46"W], 2 Aug 1972, *Croat 18710* (UC). Maynas: Rio Zumun, affluent du rio Yahuas-Yacu, affluent du rio Ampi-Yacu affluent de l'Amazone à Pebas - commune de Colonia, territoire des indiens Bora, [3°26'02"S, 72°40'29"W], 5 Jun 1978, *Barrier 1003* (UC). Requena: 10 km E from jenaro Herrera, 4°55'S, 73°35'W, 150–200 m, 19 Sep 1998, *Tuomisto et al. 13025* (UC). **Madre de Dios:** Manu: Cerro de Pantiacolla: Rio Palotoa 10-15km NNW of Shintuya, transect to ridgetop, 12°35'S, 71°18'W, 650–700 m, 11 Dec 1985, *Foster et al. 10704* (UC). Tambopata: Puerto Maldonado, trail to Aguajal, 37.5 KM west of Puerto Maldonado, highway Cusco-Puerto Maldonaro, 12°42'48"S, 69°28'11"W, 200–246 m, 20 May 2010, *Clark et al. 11562* (UC). **Pasco:** Oxapampa: Dist. Puerto Bermudez, bosque de protección San Matias San Carlos, 10°11'40"S, 74°56'30"W, 260 m, 10 Sep 2006, *Blasido & Gonzáles 128* (UC). **San Martín:** San Antonio: Progreso, village in the first valley of the Cerro Escalera, from Tarapoto after the tunnel, along Tarapoto-Yurimaguas road, 6°24'S, 76°18'W, 700 m, 8 Aug 2002, *Christenhusz et al. 2048* (UC). Tarapoto: in monte Guayrapurune, prope Tarapoto, Peruviae orientalis, [6°27'19"S, 76°12'27"W], 1856, *Spruce 4689* (P). **Ucayali:** Padre Abad: Distrito Padre Abad. Carretera al Rio Yurac, 7 km al este del Caserio La Libertad, aproximadamente 12 km de la ciudad de Aguaytia, 09°04'S, 75°36'W, 350 m, 9 Oct 2004, *Vigo & Graham 16323* (UC). **SURINAME. Nickerie:** Middenstandspolder: Area of Kabalebo Dam project, moist forest on steep slope at 3340 m in line from road km 34 wesward, [5°45'56"N, 56°47'08"W], 30–130 m, 7 Nov 1981, *Linderman*

& de Roon 785 (UC, US). **Sipaliwini:** Kabalebo: Mts Bakhuis, concession BMS: zone 1, sud. site no. 005, 4°34'N, 56°47'W, 280 m, 28 Sep 2005, *Bordenave et al. 8033* (CAY). Tapanahony: Lely Mts., airstrip, 4.16°N, 54.44°W, 600–650 m, 30 Nov 2004, *Jansen-Jacobs et al. 6892* (UC). **VENEZUELA. Amazonas:** Atabapo: 15 km aprox. al S-E de San Fernando de Atabapo, bosques muy húmedos de tierra firme em el Sector "El Pozo" em zona experimental de la CVG - proyecto Caucho, 3°55'N, 67°40'W, 110 m, 10 a 16 Jan 1988, *Stergios et al. 11518-b* (UC). Atures: Laguna El Sillón y Caño Mariguaca, 78 km NE Puerto Ayacucho, 5°49'N, 66°50'W, 400 m, Oct 1989, *Fernandes et al. 6425* (UC). Mavaca: Misión Rio Mavaca, 1°58'N, 65°6'W, 200–230 m, 3 Feb 1991, *Stergios & Yánez 15112* (UC). Rio Negro: Neblina Base Camp on Río Bario (=Río Mawarinuma), left bank, SE of Base Camp, along Bongo Trail, 00°49'50"N, 66°09'40"W, 140 m, 18 Feb 1985, *Beitel 85213* (UC). **Apure:** Pedro Camejo: Along the Río Meta at Fundo El Agarrobo, 22 airline km WNW of Buena Vista, caño 2-3 km N of Isla Algarrobo, 6°11'N, 68°47'W, 75 m, 17 Feb 1978, *Davidse & González 14294* (UC). **Bolivar:** Gran Sabana: 5 km south of San Ignacio de Yuruani, 4°59'N, 61°10'W, 850 m, 11 May 1988, *Liesner 24479* (UC). Las Cañas Bravas: Rio Suapure, [6°32'21"N, 66°39'15"W], 400–520 m, 19 Jan 1956, *Wurdack & Monachino 41294* (RB, US). Raúl Leoni: 50 km al SW de Guaiquinima y 72 km al W de Karún, 5°18'N, 63°59'W, 230 m, Nov 1988, *Fernandez & Aymard 4905* (UC). Sucre: Alrededores de Santa María de Erebato, 4°59'N, 64°49'W, 340 m, Feb 1989, *Fernandez & Sanoja 5083* (UC). Cedeño: Morichal El Caballo, ca. 225 km at S de Calcara del Orinoco by road, 6°17'N, 67°15'W, 100 m, 4 Nov 1985, *Holst & van der Werff 2573* (UC). **Delta Amacuro:** Antonio Diaz: Estribaciones de la Sierra de Imataca, 5 km al Sur de Manoa, 8°27'N, 61°20'W, 0 m, Feb 1987, *Fernandez 3770* (UC). **Táchira:** La Fundación: 10 km E of La Fundación (13-23 km by road), around Represa Dorada, [7°47'12"N, 71°46'17"W], 600–1000 m, 10 a 13 Mar 1981, *Liesner & González 10383* (UC).

Smith (1986) included *Soromanes integrifolium* Fée [=*Polybotrya serratifolia* (Fée) Klotzsch] in the synonymy of *Cyclodium meniscioides* because the illustration in the protologue of *S. integrifolium* showed a sterile frond of *C. meniscioides* mixed with a fertile frond of *P. serratifolia.* When Moran (1987) designated only the fertile frond as lectotype of *S. serratifolium*, he disregarded the admixture and fixed the application of the name concerned (Turland et al., 2018, Art. 8.2).

Cyclodium meniscioides is characterized by its subdimorphic to dimorphic 1–pinnate fronds, anastomosing veins, and peltate indusia, with ciliate margins. It mostly resembles *C.*

heterodon and *C. akawaiorum* (which see for differences). This species is highly variable in morphology, and nearly all characters seem to be plastic, and not exclusive of a specific region. In other words, we found no coorelation between these morphological characters and the geographical areas where *C. meniscioides* occur.

As for the varieties recognized for *Cyclodium meniscioides, C. meniscioides* var. *rigidissimum* and *C. meniscioides* var. *paludosum,* we found that there is a considerable number of intermediates between their extremes even in a same geographical region and, therefore, we are treating them as just variations of *C. meniscioides*.

Noteworthy is one specimen from Brazil (*Salino 412b*) that has smaller and simple sterile and fertile fronds, an unusual character in this species. The plasticity of size and number of lateral pinnae can be seen in two specimens from French Guiana (*Bordenave 7248*). In these specimens the petiole size of sterile frond has varied almost 20 cm long, and the number of lateral pinnae varied from 1 to 6 pairs.

Recently, two intergeneric hybrids involving this species were described: one from southern Amazon with *Polybotrya goyazensis* Brade – ×*Cyclobotrya telespirensis* Engels & Canestraro (Engels & Canestraro, 2017) – and another from state of Ceará with *P. osmundaceae* Humb. & Bonpl. ex Willd. – ×*Cyclobotrya amalgamata* Schwartsb. & Canestraro (Schwartsburd et al., 2018). According to Bohn et al. (in prep.), *C. meniscioides* is monophyletic and sister to *C. akawaiorum*, a clade supported by dimorphic fertile–sterile fronds and conform apical pinnae.

9. Cyclodium pubescens Bohn & Labiak, sp. nov. Type: Brazil. Mato Grosso, Itaúba, Resgate de FLORA da UHE Colíder, estrada de acesso para Lote F de supressão, 18 Aug 2016, *M. E. Engels & L. M. S. Aquino 4763* (holotype: MBM-382725; isotype: HERBAM n.v., TANG n.v.). (Figs. 1C, 6, 8B).

Plants terrestrial or root climber. *Rhizomes* short–creeping, 0.8–1.5 cm diam., with ca. 2–4 fronds per 3 cm, scaly; *rhizome scales* basifixed, lanceate, 5–15 × 0.2–0.6 mm, bicolorous, light to dark brown, with a discrete darker center, margins slightly dentate to fimbriate; *fronds* dimorphic, lanceate to lanceolate; sterile fronds (56–) 96.5–117.5 × (18–) 27–44 cm, fertile fronds (82.5–) 123–144 × 18–26 cm; *petioles* stramineous to tan, with several scales more abundant towards the base, and linear, septate, dark brown microscales, also with acicular, septate, translucent hairs, 0.5–1 mm long, (26–) 33–51.5 cm long in sterile

fronds, (46.5–) 60.5–91 cm long in fertile fronds, 2–6 mm diam.; *petiole scales* basifixed with a narrow sinus, lanceate, 3–12 × 0.2–0.5 mm, concolorous, light to dark brown, margins dentate to fimbriate; *laminae* 1–pinnate, subcoriaceous to coriaceous, with 5–9 (–12) pairs of lateral pinnae, sometimes with a reduced pinna before the apical and conform apex, (28–) 34–60 cm long in sterile fronds, (21.5–) 34–79 cm long in fertile fronds; *rachises* stramineous to tan, grooved adaxially, grooves with bacilliform, translucid, yellowish hairs, ca. 0.1–0.2 mm long, linear, septate, light to dark brown microscales, ca. 0.3–0.4 mm long, abaxially with several acicular, raised, septate, translucent hairs, sometimes with microscales similar to those of the grooves, and linear scales composed of few cells at base, ca. 2 mm long; *pinnae stalks* 2–4 (–6) mm long, with hairs, microscales and scales similar to those of the rachis; *pinnae* lanceate to lanceolate, slightly asymmetric, truncate acroscopically and cuneate basiscopically, apices acute to acuminate, margins entire to crenate, the fertile more dissected, sterile basal pinnae 13–16 (–23) × 3.5–5.5 cm, fertile basal pinnae 8.5–11.5 × 1.5–3 cm, sterile medial pinnae 12–14.5 (–17.5) × 3.5–5 cm, fertile medial pinnae 9–11.5 × 1.5–3 cm; *costae* abaxially with several acicular, raised, septate, translucent hairs, and linear, septate, dark brown microscales, also with light to dark brown scales, composed of few cells at base, ca. 1 mm long; *laminar tissue* with hairs and microscales similar to those of costa; *veins* anastomosed, inconspicuous, with 4–6 anastomoses between costa and margin, sometimes from the united veinlets there is a free tip, or the tip is united to the next veinlets; *sori* discrete, not impressed, medial on veins, forming 4–6 rows of sori between costa and margin, biseriate between two main lateral veins, often confluent; *indusia* peltate, ca. 0.5–1.5 mm diam, concolorous, light to dark brown, the margins densely ciliate, often with cilia all over the top; *spores* 60–71 × 48–64 μm, the perines perforated, broadly folded and densely echinulated, forming anastomosing areoles, the folds high and continuous.

Distribution, ecology and conservation status.— Cyclodium pubescens occurs in the western portion of the Amazon basin, in Peru (Loreto) and Brazil (Amazonas, Rondônia, and Mato Grosso states). All specimens are terrestrial, with the exception of one (*Cid 3722*) that was recorded as epiphytic over a living tree. This species is often associated to humid soils, composed of sand or clay, near streams, 130–310 m. The extent of occurrence (EOO) of *C. pubescens* is 977,660 km², and it is included as “least concern” by GeoCAT. The area of occupancy (AOO) was estimated at 36 km², which is less than the threshold of 500 km² for the endangered category (EN), under the criteria and B2 bii, biii. This species is often recorded from transitional areas between Amazonian rainforest and Brazilian Cerrado, and

area nowadays considered as the “deforestation frontier” in the southern portion of the Amazon. Considering that, *C. pubescens* is assessed here as being “endangered”.
EN B2bii, biii

Specimens examined. BRAZIL. Amazonas: Coari: Rio Urucu, base da PETROBRÁS, ca. de 20 min. de motor de popa, margem direita do rio, [4°10'10"S, 63°29'58"W], 31 May 1991, *Freitas & Mota 437* (INPA). Manaus: Reserva Florestal Adolpho Ducke, em baixio próximo ao Igarapé BOLIVIA, 2°58'S, 59°54'W, 12 Sep 2004, *Zuquim et al. 355* (INPA). Novo Japurá: Confluêcia dos rios Traira e Apapóris, próximo a cachoeira Urumutum, [1°40'54"S, 67°58'11"W], 19 Nov 1982, *Cid & Lima 3722* (INPA). **Mato Grosso:** Itaúba: Resgate de FLORA da UHE Colíder, Estrade de acesso para o Lote F de supressão. Floresta do Planalto dos Parecís, 11°07'02"S, 55°26'08"W, 310 m, 18 Aug 2016, *Engels & Aquino 4763* (MBM); Resgate de FLORA da UHE Colíder, lote G de supressão, Floresta do Planalto dos Parecís, 11°04'16"S, 55°17'27"W, 278 m, 22 Jan 2015, *Bronholi et al. Equipe 11-224* (MBM, UPCB). **Rondônia:** Porto Velho: Parque Natural Municipal de Porto Velho, 8°41'66"S, 51°45'80"W, 1 Jun 2017, *Gonçalves et al. 130* (RON). **PERU. Loreto:** Maynas: Distrito Iquitos, Carretera de Zungaro Cocha, trocha hasta um purma, cerca a la quebrada de Shushuna, [3°48'49"S, 73°21'00"W], 160 m, 19 Oct 1982, *Rimachi Y. 6354* (US); Distrito Iquitos. Puerto Almendras, [3°49'45"S, 73°23'03"W], 130 m, 26 Jul 1988, *van der Werff et al. 9789* (UC).

Cyclodium pubescens is characterized by its 1–pinnate fronds, anastomosing veins and by bearing several acicular, multicellular, translucid hairs on laminae, costa and rachis. It most resembles *C. meniscioides* in lamina size, and venation, but the hairs are lacking in C. *meniscioides*. *Cyclodium pubescens* was not included in any phylogenetic analysis, but we believe that it is probably closely related to *C. meniscioides* based on their morphological similarities.

10. Cyclodium rheophilum A. R. Sm., Amer. Fern J. 76(2): 88, f. 9A–B, 10. 1986. Type: French Guiana. Upper Oyapock, Mt. St. Marcel, torrent on the S slope, 260 m, 27 Jul 1975, *J.–J. de Granville 2586* (holotype: F-0075677F; isotypes: K-000590378, K-000590379, NY-00842334, P-00630613, UC-1542815, Z n.v.). (Figs. 1C, 3 A–C, 8C).

Plants rheophytic; *rhizomes* short–creeping, 0.3–0.7 cm diam., with ca. 8–12 (–20) fronds per 3 cm, scaly at apex; *rhizome scales* basifixed, thin, lanceolate, 2–4 × 0.5–1 mm, concolorous, light brown, margins entire to slightly fimbriate; *fronds* monomorphic to subdimorphic, linear or lanceolate to elliptic, sterile fronds 16–21 (–29) × 3.5–5 (–8.5) cm, fertile fronds (25–) 30–34 × 6.5–9 cm; *petioles* stramineous to tan, with scattered scales and several reddish–brown dots, 3–5 (–7.5) cm long in sterile fronds, 9.5–10 cm long in fertile fronds, 0.05–0.15 cm diam.; *petiole scales* basifixed with a sinus, ovate–lanceolate, appressed, 1–2.5 × 0.3–1 mm, concolorous, light brown, margins thin and entire to fimbriate; *laminae* 1–pinnate, chartaceous, with 11–18 (–21) pairs of lateral pinnae and apex pinnatifid, 7–16 (–20) cm long in sterile fronds, 20–24 cm long in fertile fronds; *rachises* stramineous to tan, rounded abaxially and grooved adaxially, the grooves with bacilliform, translucid, yellowish, hairs, ca. 0.1 mm long, abaxially with septate, linear, brown to dark brown microscales, also with lanceate, brown scales, with few cells at the base, ca. 0.5–2 mm long; *pinnae stalks* 0.5–2 mm long, glabrescent or with microscales similar to those on the rachis; *pinnae* linear to elliptic, bases truncate acroscopically and cunenate basiscopically, sometimes asymmetric at the base with a narrow subauricle at the acroscopic side, apices acute to obtuse, margins crenate to dentate, sterile basal pinnae 1.5–5 × 0.3–0.7 cm, fertile basal pinnae 2.7–4.8 × 0.4–0.5 cm, sterile medial pinnae 2.5–5 × 0.4–0.6 cm, fertile medial pinnae 3.2–5 × 0.45–0.5 cm; *costae* with septate, linear, light to dark brown microscales; *laminar tissue* with microscales similar to those of the costa, also abaxially sometimes with several reddish, resinous dots; *veins* free, inconspicuous, simple to 1–furcate between costa and margin; *sori* discrete, impressed, median on veins, forming 1 row of sori between costa and margin, uniseriate between two main lateral veins; *indusia* reniform, ca. 0.5–0.8 mm diam, bicolorous, stramineous, darker and glandular margins; *spores* 59–64 × 39–41 µm, the perines perforated, not folded, and densely echinulated.

Distribution, ecology and conservation status.—Cyclodium rheophilum is known only from French Guiana. As its name suggests, this species is rheophytic, growing on rocks associated to creeks, at 260 m. *Cyclodium rheophilum* is known from only two gatherings, which suggests it to be a rare and narrow endemic species to the Guyanas. Therefore, we have no enough information to categorize it, and it is assessed here as "data deficient".
DD

Specimens examined. FRENCH GUIANA. Arrondissement of Cayenne: Mont

Saint-Marcel: crique située au sud du massif, au dessus des cascades, 2°22'30"N, 53°00'20"W, 260 m, 27 Jul 2002, *de Granville et al. 15523* (CAY, NY, US).

Cyclodium rheophilum is characterized by the reduced fronds, conspicuous scales on costae, and peltate indusia with minutely glandular margins. This species seems to be very rare, and we were able to see only two specimens of it. In both specimens it is mentioned that this species occurs on rocks along streams, being possibly a rheophitic species.

Among the species that occur in French Guyana, the most similar ones are *C. guianense* and *C. inerme. Cyclodium rheophilum* differs from *C. guianense* by its smaller fronds (16–34 vs. 55–140 cm long), and spores with non–folded and perforated perines (vs. folded and non–perforated in *C. guianense*). Some specimens of *C. guianense* are more similar to *C. rheophilum* by reduced fronds and narrower pinnae (see comments under *C. guianense* for further comments). From *C. inerme, C. rheophilum* differs by the presence of costal scales, and by its non–folded and perforated perines (vs. folded and non–perforated). *Cyclodium rheophilum* was included in a phylogeny by Bohn et al. (in prep.), where it was recovered in an unresolved clade with *C. guianense* (which see for further discussion).

11. Cyclodium seemannii (Hook.) A. R. Sm., Amer. Fern J. 76(2): 89. 1986. *Aspidium seemannii* Hook., Sp. Fil. 4: 34, t. 230. 1862. *Polystichum seemannii* (Hook.) J. Sm., Hist. Fil. 220. 1875 (as “semani”). *Dryopteris seemannii* (Hook.) Kuntze, Revis. Gen. Pl. 2: 813. 1891. Type: Colombia. Dept. Chocó: Bay of Ardita, Dec 1947, *Seemann s.n.* (lectotype, designated by Smith, 1986: K-000590380; isolectotypes: P-00630611, P-00630612]). (Figs. 1B, 4A–G, 8D).

Plants terrestrial; *rhizomes* short–creeping, 0.5–1 cm diam., with ca. 7–14 fronds per 3 cm, scaly; *rhizome scales* basifixed with a sinus, thickened, slightly raised and overlapping, sometimes with a creased center, cordiform, 1.5–3 × 0.3–0.7 mm, concolorous, dark brown to black, margins entire; *fronds* monomorphic to subdimorphic, lanceolate–ovate, sterile fronds 49–61 × 23–27 cm, fertile fronds 49–61 × 23–27 cm; *petioles* stramineous to tan, with scattered scales, and septate, linear, golden to light brown microscales, also with bacilliform, translucid, yellowish hairs, 20–38 (–48.5) cm long in sterile fronds, 20–38 (–48.5) cm long in fertile fronds, 2–4 mm diam.; *petiole scales* basifixed with a narrow sinus, cordiform, 1.5–3 × 0.3–0.6 mm, concolorous, light brown to brown, margins entire; *laminae* 1–pinnate–

pinatissect to 3–pinnate, subcoriaceous, with 12–18 pairs of lateral pinnae, apex gradually reduced and pinnatifid, 28–29 (–53) cm long in sterile fronds, 28–29 (–53) cm long in fertile fronds; *rachises* stramineous to tan, rounded abaxially and grooved adaxially, the grooves with several bacilliform, translucid, blackish hairs, ca. 0.1 mm long, abaxially with septate, linear, light brown microscales, and lanceate to cordate, dark brown scales, ca. 1–2 mm long, and some smaller scales with few cells at the base, 0.3–0.8 mm long, also with bacilliform, translucid, yellowish hairs, and several multicellular, acicular, translucid hairs; *pinnae stalks* 5–8 mm long, with hairs and microscales similar to those of the rachis; *pinnae* linear to lanceolate or elliptic, with ca. 8–14 pairs of lateral pinnules, bases asymmetric, with the first segment larger and arising acroscopically, sometimes at the base with an expanded auricle at the acroscopic side, often 3–pinnate, apices pinnatifid, sterile basal pinnae 12–18.5 (–22) × 4.5–7.5 cm, fertile basal pinnae (8.5–) 14.5–23.5 × (2.7–) 5–8 cm, sterile medial pinnae 9–14 × 2–3 cm, fertile medial pinnae (7–) 11.5–14 × (1.5–) 2.5–3.5 cm; *costae* abaxially with hairs, scales and microscales similar to those of the rachis, sometimes with sessile, globose, yellowish to reddish glands; *laminar tissue* with hairs, scales, microscales and glands similar to those of the costae; *pinnules* elliptic to slightly spathulate, bases larger acroscopically and cuneate basiscopically, asymmetric at the base with an expanded auricle at the acroscopic side, apices obtuse to round and crenate to serrate, margins crenate to pinnatifid, sterile basal pinnules 2–3 × 0.7–1 cm, fertile basal pinnules 1.5–4 × 0.5–1.5 cm; *costules* abaxially with septate, linear, reddish–brown microscales, more frequent towards base of pinnule; *veins* free, inconspicuous, 7–10 furcate between costa and margin; *sori* discrete, inconspicuous, terminal on veins, forming 6–10 rows of sori between costa and margin, uniseriate or bisseriate between two main lateral veins; *indusia* subpeltate to peltate, ca. 1–2 mm diam, concolor, stramineous, margins and surface with several glandular trichomes; *spores* 52–54 × 39–44 μm, the perines non–perforated or not, broadly folded and densely echinulated, the folds high and continuous.

Distribution, ecology and conservation status.—Cyclodium seemannii is restricted to the pacific coasts of Colombia and Ecuador. In Colombia, it is present in both highly humid (Chocó, San Juan River), and dryer (Pacific Coast) regions (sensu Forero & Gentry, 1989). All specimens are terrestrial, occurring in wet evergreen forests, more rarely in swamps, between 0–680 m. The extent of occurrence (EOO) of *C. seemannii* is 41,883 km², recovered as “near threatened” by GeoCAT. The area of occupancy (AOO) was estimated at 36 km², indicating it as “endangered” under criterion B2 bii, biii. *Cyclodium seemannii* seems to be

under-collected, as well as *C. chocoense*, that overlaps in the distribution in Chocó and northwestern Ecuador. Different from the latter, *C. seemannii* occurs in a more restricted area, that seems to be more disturbed, and presents a narrower altitudinal range. Therefore, it is assessed here as "endangered".

EN B2bii, biii

Specimens examined. COLOMBIA. Chocó: On left bank of river Baudo, about 1.5 km upstream of estuary, practically opposite the easternmost houses of Puerto Pizarro, about 500 meters south-east of river bank in the depression-area of the Estero del Medio, [4°57'53"N, 77°20'25"W], 0 m, 16 Feb 1967, *Torres-Romero et al. 21904* (UC). **Nariño:** Barbacoas: Resguardo Indígena de Saundé, Peña Blanca, orillas de la quebrada Saundé, 1°30'N, 78°20'W, 350 m, 19 Jan 1996, *Ramírez et al. 9611* (UC); Corregimiento El diviso a 27 km Del Diviso, quebrada la Angosta, margem izquierdo de la carretera vía Diviso-Tumaco, [1°24'47"N, 78°14'39"W], 680 m, Mar 1995, *Fernández et al. 12473* (COL). **ECUADOR. Carchi-Esmeraldas:** Near Lita, [0°49'27"N, 78°26'49"W], 600 m, 19 May 1987, *van der Werff et al. 9492* (UC). **Esmeraldas:** Lita-San Lorenzo Road, 18 km W of Río Lita Bridge (on old road below Lita), 6.6 km W of bridge over Río Chuchubí, site near Alto Tambo, 0°52'11"N, 78°27'16"W, 425 m, 10 Jul 1998, *Croat et al. 82622* (UC); Road Lita - San Lorenzo (under construction), km. 34.4, 00°52'N, 78°31'W, 650 m, 28 Sep 1991, *Ollgaard 99163* (P). San José: km 321 along railroad from Ibarra to San Lorenzo, 1°N, 78°W, 350 m, 3 May 1982, *Boom 1308* (NY). San Lorenzo: "Proyecto NO", at the end of new road (km 14), [1°17'04"N, 78°50'21"W], 18 Aug 1967, *Sparre 18187* (NY); Parroquia de Concepcion, Playa Rica, [0°58'25"N, 79°38'20"W], 105 m, 16 Dez 1936, *Mexia 8452* (US).

Cyclodium seemannii is characterized by its thick, overlapping rhizome scales, dense indument on petioles, rachis and costa, and also by bearing at least some round–reniform indusia, with ciliate margins and surfaces. *Cyclodium seemannii* most resembles *C. trianae,* from which it differs by its cordiform, blackish rhizome scales that are creased at center, and presence of multicellular, acicular and translucid hairs on costa and rachis. Moreover, these two species are parapatric. It also resembles *C. chocoense* (see comments under that species), with which it overlaps in distribution. Unfortunately, *C. seemannii* was not included in the molecular phylogenetic study conducted by Bohn et al. (in prep.), so its phylogenetic placement remains unknown. On the basis of morphology alone, we suspect that it will be more closely related to the clade comprising *C. chocoense* and *C. trianae*.

12. Cyclodium trianae (Mett.) A. R. Sm., Amer. Fern J. 76(2): 92, f. 13D–F. 1986. *Aspidium trianae* Mett., Ann. Sci. Nat., Bot., sér. 5, 2: 243. 1864. *Nephrodium trianae* (Mett.) Baker, Syn. Fil. 286. 1867. *Dryopteris trianae* (Mett.) Kuntze, Revis. Gen. Pl. 2: 814. 1891. Type: Colombia. Nova Granada: Prov. Barbacoas; via de Túquerres, May 1853, *J. J. Triana 32* (lectotype, designated by Smith, 1986: B-200076883; isolectotype: BM-000937908 [also numbered as 615], UC n.v., US n.v.).

Nephrodium firmifolium Baker, Syn. Fil., ed. 2. 501. 1874. *Dryopteris firmifolia* (Baker) Kuntze, Revis. Gen. Pl. 2: 812. 1891. Type: Peru. "In monte Guayrapurima, prope Tarapoto, Peruviae orientalis", Aug 1856, *R. Spruce 4662* (lectotype, designated by Smith et al., 1986: K-000200351; isolectotypes: BM-000777108, BM-000777109, BR n.v., P-00630608, P-00630609]). (Figs. 1B, 4H–M, 8E).

Plants terrestrial; *rhizomes* short–creeping, 0.6–0.8 cm diam., with ca. 5–7 fronds per 3 cm, scaly; *rhizome scales* basifixed, lanceate, 5–10.5 × 0.1–0.5 mm, concolorous, light brown, apices twisted and entire or slightly fimbriate, margins entire; *fronds* monomorphic, lanceolate–ovate or elliptic, sterile fronds 72–83.5 × 27–34 (–47) cm, fertile fronds 102–152 × 33–47 cm; *petioles* stramineous to tan, darker at base, with scales and microscales more abundant towards the base, 35.5–40.5 (–59) cm long in sterile fronds, 54–85 (–105.5) cm long in fertile fronds, 4–8 mm diam.; *petiole scales* basifixed with a sinus, cordate at base and abruptly reduced to a filiform middle and apex, 3–10 × 0.4–0.8 mm, concolorous, light to dark brown, apices twisted, margins dentate to ciliate; *laminae* 1–pinnate–pinnatisect to 2–pinnate, rarely 3–pinnate, chartaceous to subcoriaceous, with ca. 16–18 pairs of lateral pinnae and apex pinnatifid, 36–42.5 cm long in sterile fronds, 48.5–63 cm long in fertile fronds; *rachises* stramineous, with lanceate scales, composed of few cells at the base, 0.5–2 mm long, and septate, linear, brown, scattered microscales; *pinnae stalks* 5–7 (–9) mm long, with bacilliform, translucid, yellowish hairs, also with scales and microscales similar to those of the rachis; *pinnae* linear to lanceolate–ovate or elliptic, with ca. 9–15 pairs of lateral pinnules, bases asymmetric, with the first segment larger and arising acroscopically, apices pinnatifid and crenate to dentate, sterile basal pinnae 14–20 × 4.5–5 cm, fertile basal pinnae 16–23 × 4.5–6.5 cm, sterile medial pinnae 12–13 × 3–4 cm, fertile medial pinnae 14.5–19 × 2.5–5 cm; *costae* abaxially with scales and microscales similar to those of the rachis; *laminar tissue* with microscales similar to those of the costa; *pinnules* lanceolate to elliptic, bases truncate

acroscopically and frequently attached to costae basiscopically, apices acute or rounded, margins crenate, 2–4 × 0.5–1.3 cm in sterile fronds, 3–4 × 0.7–1 cm in fertile fronds; *costules* with scales and microscales similar to those of the costa; *veins* free, inconspicuous, 1–2 (–4) furcate between costa and margin; *sori* discrete, impressed, median on veins, forming 8–12 rows of sori between costa and margin, uniseriate between two main lateral veins; *indusia* subpeltate to peltate, ca. 0.5–1.5 mm diam, concolorous to bicolorous, stramineous to black, with a darker center, entire to undulate margins; *spores* 39–47 × 30–39 µm, the perines perforated, broadly folded and densely echinulated, the folds high and continuous.

Distribution, ecology and conservation status.—Cyclodium trianae occurs in Panama, Colombia, Ecuador, and Peru. In South America, it is mostly restricted to the eastern side of the Andes, with the exception of a few records from northern Colombia (Antioquia and Putumayo departments). All specimens are terrestrial occurring in wet evergreen forests, between 100–1150 m. The extent of occurrence (EOO) of *C. trianae* is 1,326,196 km², recovered in the least concern category by GeoCAT analysis. The area of occupancy (AOO) was estimated at 112 km², suggesting it to be "endangered" under criterion B2 bii. Like other species that occurs in this region, *C. trianae* seems to be under-collected. Nevertheless, the species is often recorded in primary or secondary forests, with a wide altitudinal range. Considering the ecology and the large EOO of this species, it is likely that its AOO trespass the threshold of the threatened categories. *Cyclodium trianae* is assessed as "least concern". **LC**

Specimens examined. COLOMBIA. Antioquia: Anorí: between Providencia and Alhibe, 7°04'31"N, 75°08'48"W, 400–800 m, 20-25 Feb 1976, *Soejarto et al. 4457* (HUA); Vereda Madre Seca, quebrada Espíritu Santo, 07°15'12.6"N, 75°02'35.8"W, 700 m, 20 Feb 2004, *Rodríguez et al. 4517* (NY); Vereda Puntiadero o la Concha abajo, quebradas El Salto y El Claro, sector la Concha abajo, 7°17'01.2"N, 75°05'17.1"W, 720 m, 16 Jan 2004, *Rodríguez et al. 4456* (HUA); Vereda San Antonio, finca "El Cielo", alrededor de la casa, 07°16'00.5"N, 75°03'51.9"W, 690 m, 8 Nov 2003, *Rodríguez et al. 4210* (COL, HUA, NY). Cáceres: 7 km noroeste de Cáceres, sobre troncal de la Paz, [7°34'36"N, 75°20'53"W], 110–130 m, 5 Nov 1987, *Alberláez et al. 198* (HUA, NY). El Doce: 215 km de Medellín, [7°26'50"N, 75°18'24"W], 300 m, 23 Apr 1977, *Callejas 154* (HUA). San Luis: autopista Medellín-Bogotá, 8.1 Km este del puentes sobre el Rio Caldera, [6°01'34"N, 74°58'25"W], 980–1020 m, 13 Mar 1983, *de Escobar 3322* (HUA). **Bolívar:** Santa Rosa: Guamoco, Sector Las Brujas,

7°38'29"N, 74°28'57"W, 884 m, 30 Apr 2010, *Colorado et al. 357* (HUA). **Cauca:** Santa Rosa: Inspección de Santa Marta. Vereda Diamante Alto, 1°14'N, 76°36', 1050–1150 m, 22 Jun 2002, *Ramírez et al. 16001* (COL); La Piedra, Serrania de los Churumbelos, Bota Caucana, 1°13'59.32"N, 76°31'58.24"W, 1100 m, 4 Aug 1998, *Gonzáles 497* (COL); Río Nabueno, Serrania de los Churumbelos, Bota Caucana, [1°42'26"N, 76°36'51"W], 400 m, 27 Jul 1998, *Gonzáles 421* (COL); Em la orilla opuesta Pto. Limón-Rio Caquetá. Loma de José Maria y Negro Agapito, [1°02'11"N, 76°32'30"W], 300–350 m, 27 Nov 1967, *Mora 4409* (COL). Ibid., [1°02'11"N, 76°32'30"W], 300–350 m, 27 Nov 1967, *Mora 4420* (COL). **Guainia:** Barranco Minas: Serrania Caparro, Base del cerro, [3°29'13"N, 69°48'31"W], 402 m, 2 May 2014, *Diaz & Beltran 0056* (COL). **Putumayo:** Orito: Resguardo indígena Cañaveral Miraflores, finca Alto Bonito La Esperanza, 0°44'32.9"N, 76°48'29.8"W, 452 m, 20 Nov 2013, *Rodríguez et al. 8030* (NY). **ECUADOR. Napo:** Canton Tena, Jatun Sacha Biological Station, 8 km east of Misahualli, 1°04'S, 77°36'W, 400 m, 9-19 Dez 1990, *Fay & Fay 2796* (UC); Km 109.2 along the road transversing Yasuní National Park, 0°59'S, 76°12W', 200–300 m, 19 Mar 1998, *Tuomisto & Ruokolainen 11910* (UC). **ECUADOR. Napo-Pastaza:** Near Canelos, [1°35'58"S, 77°44'07"W], 300–400 m, 9 Feb 1935, *Mexia 6894* (UC, US). **Pastaza:** Rio Bobonaza, 02°07'S, 76°55'W, 300 m, 17 Jul 1980, *Ollgaard et al. 34528* (UC). **PANAMA. Panama:** Cerro Jefe, [9°14'03"N, 79°21'08"W], 900 m, 24 Jan 1996, *Galdames et al. 2432* (COL, US). Chepo: Carretera El Llano Carti, 9°16'44"N, 78°57'34"W, 400 m, 14 Jul 2012, *Salino et al. 15487* (BHCB). **San Blas:** Campamento Nusagandi, sendero Uma Ugar em la carretera, el Llano-Cartí a 19 km de la Bía Interamericana, [9°25'51"N, 78°58'38"W], 350–400 m, 27 Aug 1987, *Herrera & Irvine 339* (UC); El Llano-Cartí Road, 19.1 km from Interamerican Highway, 9°19'N, 78°55'W, 350 m, 29 Oct 1984, *de Nevers 4119* (UC). **PERU. Amazonas:** Imaza: Comunidad Aguaruna de Putuim, arriba (oeste) Pueblo de Putuim, 4°55'S, 78°19'W, 680 m, 12 Jun 1996, *Rodríguez R. et al. 978* (NY, UC). Condorcanqui: Distrito El Cenepa, Comunidad de Tutino, 04°33'05"N, 78°12'54"W, 500 m, 20 Jul 1997, *Rojas et al. 102* (NY). **Loreto:** Maynas: Explorama/ACEER reserve, 0.5-1.6 km E of the mouth of Quebrada Sucusari at lower Napo, 3°15'N, 72°54'W, 100–200 m, 21 Jan 1995, *Tuomisto et al. 7294* (NY); Balsapuerto (lower Rio Huallaga basin), [5°49'48"S, 76°33'51"W], 350–550 m, 29 Aug 1929, *Killip & Smith 28540* (US). **Pasco:** Oxapampa: Palcazu Valley, Iscozacin, 10°12'S, 75°15'W, 400 m, 25 Jan 1984, *Foster et al. 9498* (NY).

Cyclodium trianae is characterized by its long fertile fronds (102–152 cm long), and

free veins. It belongs to a group with highly dissected lamina (1–pinnate–pinnatisect to 3–pinnate), which includes *C. chocoense* and *C. seemannii* (see comments under these species for differences). Smith (1986) and Moran (1987) indicated *C. trianae* as a possible link of the relationship between *Cyclodium* and *Polybotrya* based on morphology and anatomy of petiole. Besides the highly dissected laminae and free veins, Moran (1987) found that *C. trianae* has vascular bundles shaped as a mushroom (as seem in a cross section of the petiole bases), with the base of the mushroom oriented adaxially, a trait also found in *Polybotrya*. The phylogenetic analyses performed by Bohn et al. (in prep.), support its placement within *Cyclodium,* with *C. trianae* and *C. chocoense* forming a clade that is sister to the remaining species of *Cyclodium.*

13. Cyclodium varians (Fée) A. R. Sm., Amer. Fern J. 76(2): 94, f. 9G–K. 1986.
Nephrodium varians Fée, Mém. Foug. 11: 88, t. 24, f. 2. 1866. *Dryopteris varians* (Fée) Kuntze, Revis. Gen. Pl. 2: 814. 1891. *Stigmatopteris varians* (Fée) Alston, Bull. Misc. Inform. Kew 1932(7): 309. 1932. *Thelypteris varians* (Fée) C. F. Reed, Phytologia 17(4): 323. 1968. *Cyclodium varians* C.V. Morton ex Vareschi, Fl. Venez. 1: 368. 1969, nom. nud. Type: Trinidad and Tobago. La Trinité, s.d., *M. Germain s.n.* (holotype: P-00630607]). (Figs. 1C, 3K–N, 8F)

Plants terrestrial or root climber; *rhizomes* short–creeping, 0.5–0.8 cm diam., with ca. 4–6 fronds per 3 cm, scaly; *rhizome scales* basifixed, lanceate, 2–5 × 0.3–1 mm, concolorous, dark brown to black, apices frequently twisted, margins denticulate; *fronds* monomorphic to subdimorphic, elliptic to lanceolate; sterile fronds 36–50.5 (–83) × 17–18.5 (–28) cm, fertile fronds (33.5–) 45.5–75 (–102) × 10–19 (–26) cm; *petioles* stramineous to tan or dark brown, with scales more abundant towards the base, also with septate, linear, brown microscales, and bacilliform, translucid, yellow to brownish hairs, 12–19.5 (–33) cm long in sterile fronds, 17–36.5 (–42) cm long in fertile fronds, 1–3 (–5) mm diam.; *petiole scales* basifixed, lanceate, 2.5–5 (–6) × 0.2–0.5 mm, concolorous, dark brown to black, apices twisted, margins denticulate; *laminae* 1–pinnate, subcoriaceous to coriaceous, with 8–14 (–15) pairs of lateral pinnae and apex subconform apex with a subauricule at base, 22.5–27.5 (–50.5) cm long in sterile fronds, 19–37 (–62) cm long in fertile fronds; *rachises* stramineous, rounded abaxially and grooved adaxially, the grooves with bacilliform, translucid, yellowish, hairs, ca. 0.1 mm long, also with septate, linear, dark brown, scattered microscales and hairs similar to those of

the grooves; *pinnae stalks* 1–3 (–7) mm long at basal pinnae, with bacilliform, translucent, yellowish hairs, also with microscales similar to those of the rachis; *pinnae* linear to lanceolate, bases truncate acroscopically and cuneate basiscopically, apices acute and crenate to serrate, margins entire to dentate, sterile basal pinnae 6–9.5 (–14.5) × 1.3–2.2 (–2.5) cm, fertile basal pinnae (4–) 5.5–13.5 (–19.5) × (0.6–) 1–1.5 (–4) cm, sterile medial pinnae 8–9 (–15) × 1.1–1.5 (–2) cm, fertile medial pinnae 5.5–12× 0.7–1.5 cm; *costae* abaxially with linear to lanceolate, brown scales, sometimes with few cells at base, and septate, linear, brown microscales; *laminar tissue* with microscales similar to those of the costae; *veins* anastomosed, conspicuous, with 2–3 anastomoses between costa and margin; *sori* discrete, impressed, forming 1–3 rows of sori between costa and margin, biseriate between two main lateral veins, sometimes connivent towards costa; *indusia* peltate, round, ca. 0.7–1 mm diam, concolorous or bicolorous, brown or sometimes with a darker center, ciliate margins; *spores* 51–63 × 37–47 µm, the perines perforated, broadly folded, and densely echinulated, the folds high and continuous.

Distribution, ecology and conservation status.—Cyclodium varians is known from Guyana, Venezuela (first record), and Trinidad. Most examined specimens were collected from 1895 to 1986, only two collections are recent (2003). Just three gatherings bear comments about the habit of this species: one terrestrial (*Clarke 9964*, US), one epiphytic (*Clarke 10037,* NY), and a creeping rhizome (*Holst 2643,* UC). As observed by Smith (1986), most of the rhizomes do not appear to have been buried in the ground and seem to be vertical, resembling the creeping habit of *C. meniscioides* and *C. akawaiorum*. Furthermore, Smith (1995) described *C. varians* as "hemiepiphytic or terrestrial along muddy creek banks", and most specimens seem to be associated to rivers, from 500 to 625 m. One exception is *Britton 1941* (US), which was recorded as living in Aripo savanna. The extent of occurrence (EOO) of *C. varians* is 142,214 km², recovered as "least concern" by GeoCAT. The area of occupancy (AOO) was estimated at 40 km², suggesting it to be "endangered" under criterion B2 bii, biii, biv. Besides the Guianas, this species also extends its distribution to the Trinidad Island, which makes its EOO higher than the threshold for threatened categories. However, most of the collections were made over 100 ago, with little information on its ecology. Therefore, *Cyclodium varians* is assessed here as being "endangered".

EN B2bii, biii, biv

Specimens examined. GUYANA. Demerara: Essequibo, [6°43'22"N, 58°29'51"W], 1895, *Jenman s.n.* (NY-02859617). [NY02859617]); Malali, [6°08'17"N, 58°14'17"W], 1895, *Jenman s.n.* (NY-02859616]); Mazaruni River, [6°23'50"N, 58°40'45"W], 1899, *Jenman s.n.* (NY-02859618]); s.l., [6°45'14"N, 58°26'16"W], 1895, *Jenman s.n.* (NY-02859623]); s.l., [6°45'14"N, 58°26'16"W], 1895, *Jenman s.n.* (NY-02859624). **Potaro-Siparuni:** Upper Potaro River, 5.5 km NE of Mt. Wokomung, 5°9'57.2"N, 59°46'40.8"W, 620 m, 19 Jun 2003, *Clarke et al. 10037* (NY); Upper Potaro River, Malek Falls, below new Ayanganna airstrip, 5°16'56"N, 59°49'25.7"W, 625 m, 17 Jun 2003, *Clarke et al. 9964* (US); Kamakusi mountain, upper Mazaruni River, [5°52'N], 59°50'W, 23-29 Nov 1922, *de la Cruz 2880* (F, NY, UC). **TRINIDAD.** British West Indies, border of forest strem, Aripo savanna, [10°36'41"N, 61°11'32"W], 14 Apr 1921, *N. L. Britton & E. G. Britton 1941* (US); s.l., [10°21'48"N, 61°14'13"W], 9 Feb 1910, *Christ 1903* (P-01435860]). **VENEZUELA. Bolívar:** Piar: Rio Aparamán, at rapids of Yuray-merú, tributary of Río Acanan, SW base og Amaruay-tepui, E of Auyan-tepui, W of Aparaman-tepui, small tributary of river, densely forested with trees 20-30 m high., 5°55'N, 62°15'W, 500 m, 21 Apr 1986, *Holst & Liesner 2643* (UC).

Cyclodium varians is characterized by its dark brown to black rhizome scales with twisted apices, 1–pinnate fronds and anastomosing veins. It resembles *C. akawaiorum* and *C. meniscioides* but overlaps in distribution only with the latter. *Cyclodium varians* differs from these two species by its smaller rhizome scales (2–5 mm long vs. 5–10.5 mm long in *C. akawaiorum,* and 4–15 mm long in *C. meniscioides*) that are twisted at the apex.

Cyclodium varians is also variable in division and length of its pinnae, sometimes also resembling *C. guianense* or *C. heterodon*. For instance, *Jenman s.n.* (NY-02859624) has wider and longer pinnae with deeply pinnatifid margins at the base (resembling some specimens of *C. heterodon* from northeastern Brazil), but the pinnae towards the apex are more like others of *C. varians*, decreasing to an atypical small and pinnatifid apex. Other specimen (*Jenman s.n.*, NY-02859623) was annotated as "*Cyclodium* sp. or hybrid" by Smith in 1985–86, with a larger number of lateral pinnae, and commissural vein (as *C. akawaiorum*), but lanceate pinnae with serrulate margins (as *C. varians*). Most specimens have conform apical pinnae, with no gradual pinna reduction towards the apex, as *C. meniscioides*, but some from Guyana have subconform to pinnatifid apex (*Jenman s.n.,* NY-02859617, NY-02859618). Whether these specimens represent hybrids of *C. varians* and other species of this complex is still awaiting further studies. Likewise, the phylogenetic

relationships of *C. varians* remains unknown.

Acknowledgments

We thank the CAY, INPA, MBM, NY, P, RB, RON, UC, UFP, UPCB and US Herbaria for sending us specimens on loan. We also thank Felipe Cardona (HUA), Fernanda dos Santos (JOI), Libing Zhang (MO), Liz Brogan (K), Maria Salete Marchioretto (PACA) and Olof Ryding (C) for digital images of specimens that were sent. The line drawings were prepared by Diana Carneiro. We also thank Raquel C. Marra for operating the SEM at Universidade Federal do Paraná and Duane Fernandes Lima for the help with conservation status. This project was supported by a fellowship from CAPES to AB, granted from CNPq to PHL (307514/2016–1).

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Fig. 1. Distribution of *Cyclodium* in the Neotropics.

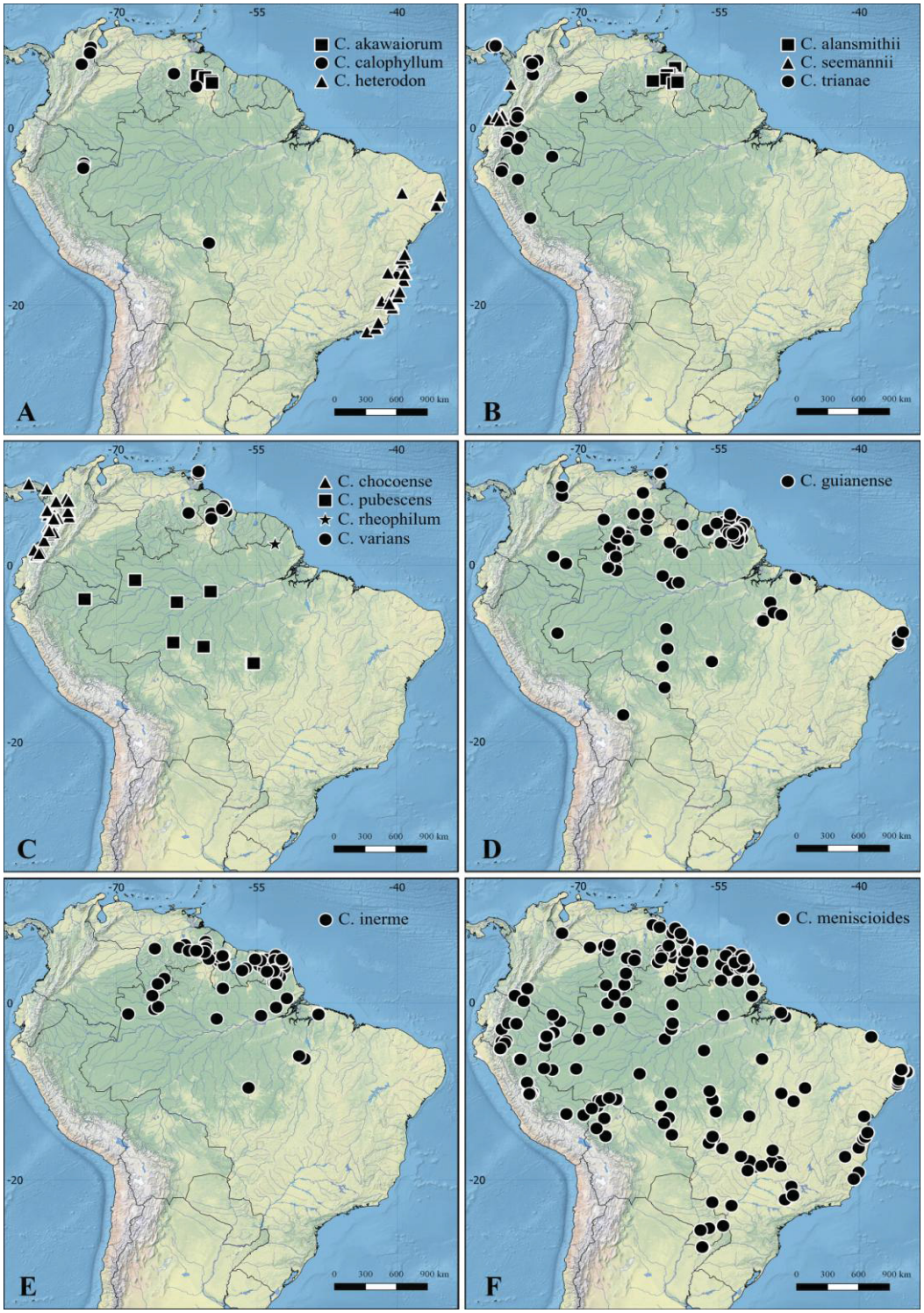

FIG. 2. *Cyclodium heterodon* (A–D) and *C. meniscioides* (E–H). **A.** Frond apex. **B.** Detail of veins abaxially. **C.** Indusium. **D.** Rhizome scale. **E.** Frond apex. **F.** Detail of veins abaxially. **G.** Fertile pinna. **H.** Indusium. (A–D from *F. B. Matos et al.* 228, UPCB and *P. Fiaschi et al. 2938*, UPCB; E–H from *J. G. Jardim et al. 4843*, UPCB and *P. H. Labiak et al. 3706*, UPCB).

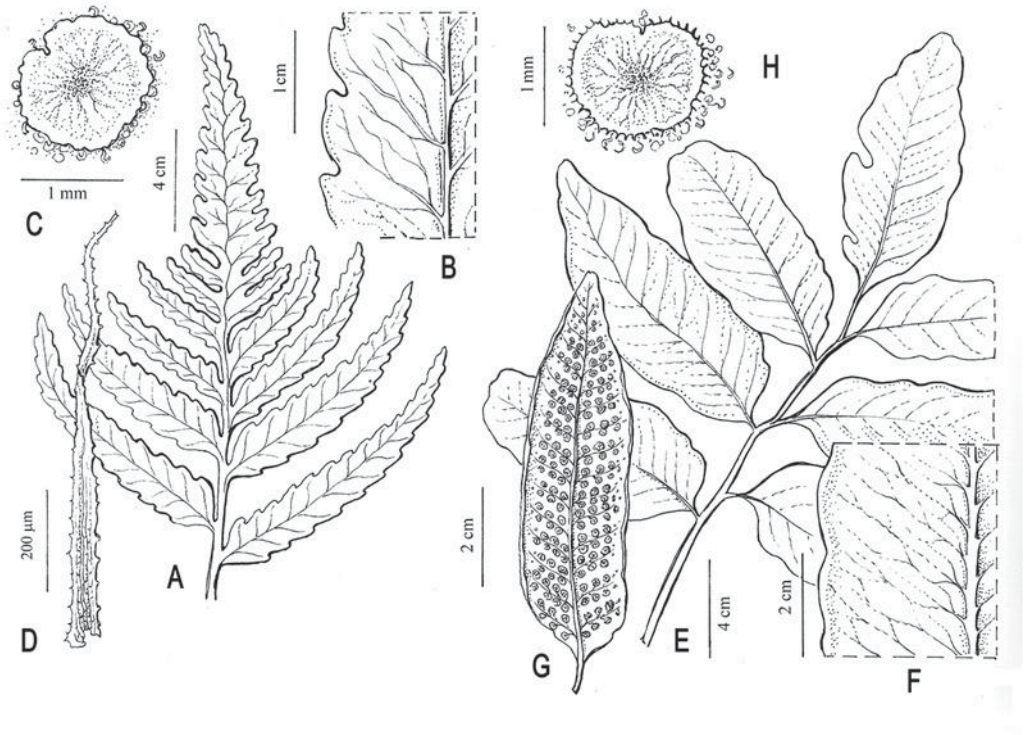

FIG. 3. *Cyclodium rheophilum* (A–C), *C. akawaiorum* (D–G)*, C. calophyllum* (H–J)*, C. varians* (K–N)*, C. inerme* (O–Q) and *C. guianense* (R–T)*.* **A.** Fertile pinna with detail of indusium. **B.** Detail of scales of pinnule and costa abaxially. **C.** Rhizome scale. **D.** Sterile pinna. **E.** Detail of scales of pinna stalk and costa abaxially. **F.** Fertile pinna with detail of indusium. **G.** Rhizome scale. **H.** Sterile pinna. **I.** Fertile pinna with scales and detail of indusium. **J.** Rhizome scale. **K.** Frond apex. **L.** Fertile pinna with detail of indusium. **M.** Sterile pinna. **N.** Rhizome scale. **O.** Fertile pinna. **P.** Fertile pinna with detail of indusium. **Q.** Rhizome scale. **R.** Sterile pinna. **S.** Fertile pinna with detail of indusium. **T.** Sterile pinna with detail of costal scales. (A–C from *Granville 15523*, NY; D–G from *H. D. Clarke et al. 9150,* CAY, and *K. E. R. 1207*, UC; H–J from *B. Stergios 10604*, UC, and *R. Liesner* & *A. González 13307*, UC); K–N from *H. D. Clarke et al. 9964* [US] and *10037* [NY]; O–Q from *Cremers 7828,* CAY and *J. J. de Granville et al. 12708,* CAY; R–T from *Cremers et al. 10271*, UC and *M. S. da Costa 33,* UPCB).

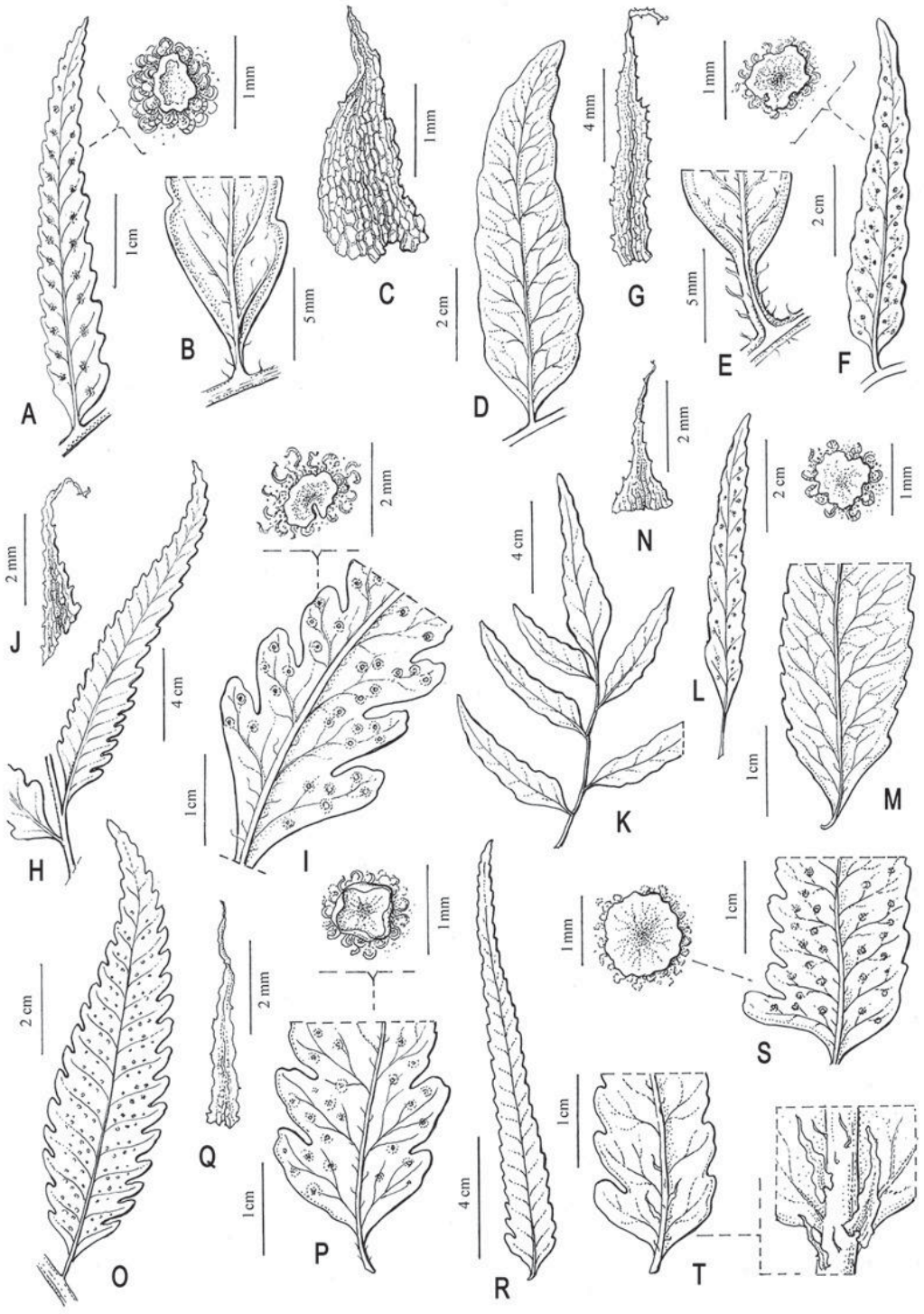
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FIG. 4. *Cyclodium seemannii* (A–G), *C. trianae* (H–M) and *C. chocoense* (N–R). **A.** Sterile frond. **B.** Detail of costa abaxially. **C.** Fertile pinnule. **D.** Fertile pinnule with detail of veins and soral distribution. **E.** Indusium. **F.** Petiole scale. **G.** Rhizome scale. **H.** Sterile pinna. **I.** Detail of costa abaxially. **J.** Fertile pinnule. **K.** Indusium. **L.** Petiole scale. **M.** Rhizome scale. **N.** Sterile pinna. **O.** Detail of pinna stalk. **P.** Fertile pinnule. **Q.** Indusium. **R.** Rhizome scale. (A–G from *B. Øllgard 99163*, P and *Y. Mexia 8452,* US; H–M from *Rojas et al. 102*, NY and *W. D. Rodríguez et al. 4210*, NY; N–R from *W. S. Alverson et al. 143*, NY and *W. S. Hoover et al. 3935*, UC).

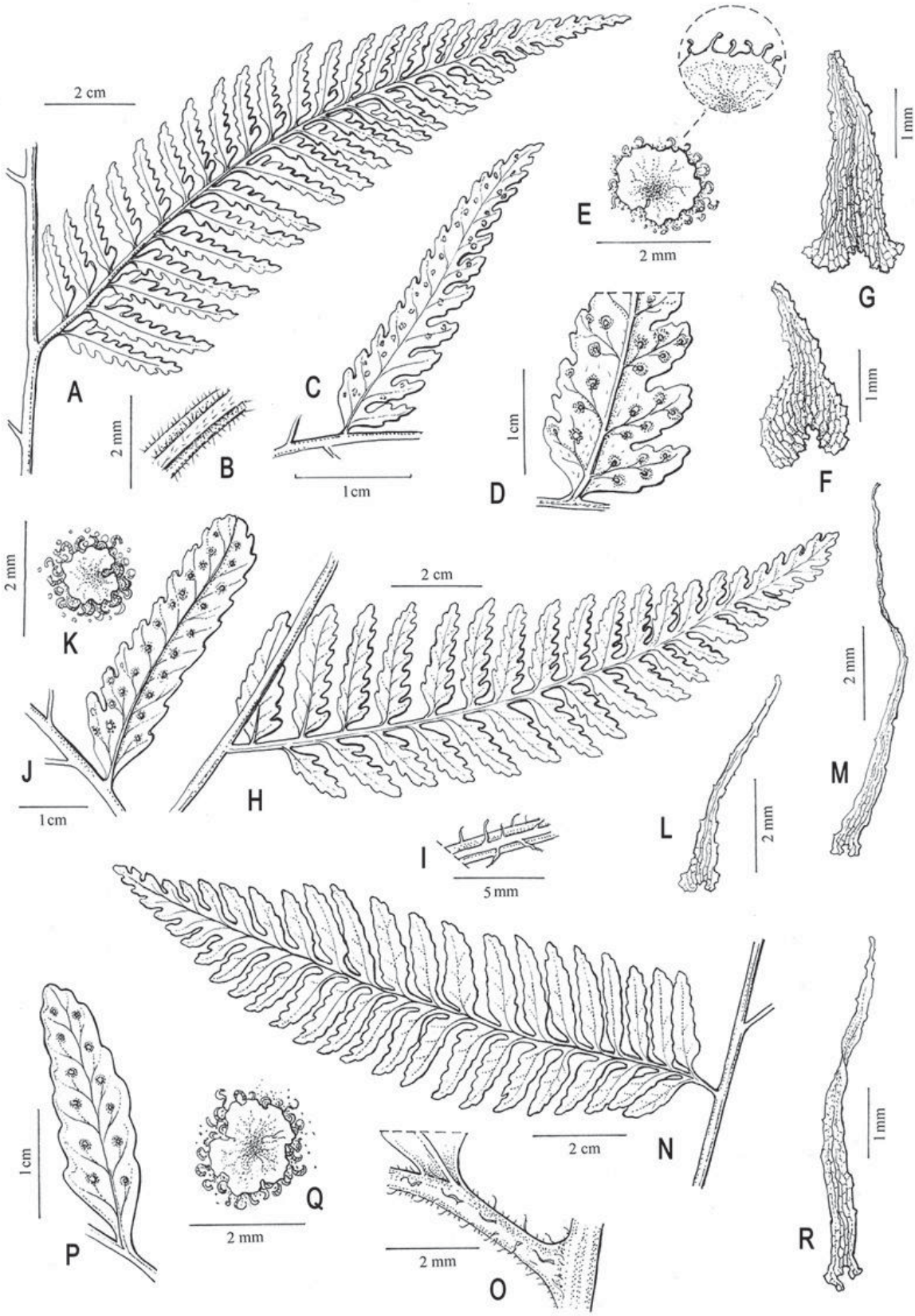
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FIG. 5. *Cyclodium alansmithii*. **A.** Habit with detail of rachis abaxially. **B.** Fertile pinna. **C.** Detail of veins. **D.** Detail of rachis adaxially. **E.** Indusium. **F.** Lateral view of peltate indusium and sporangia. (A–F from *Tillet 44942* (NY, US)). Originally from Bohn et al. (in press.).

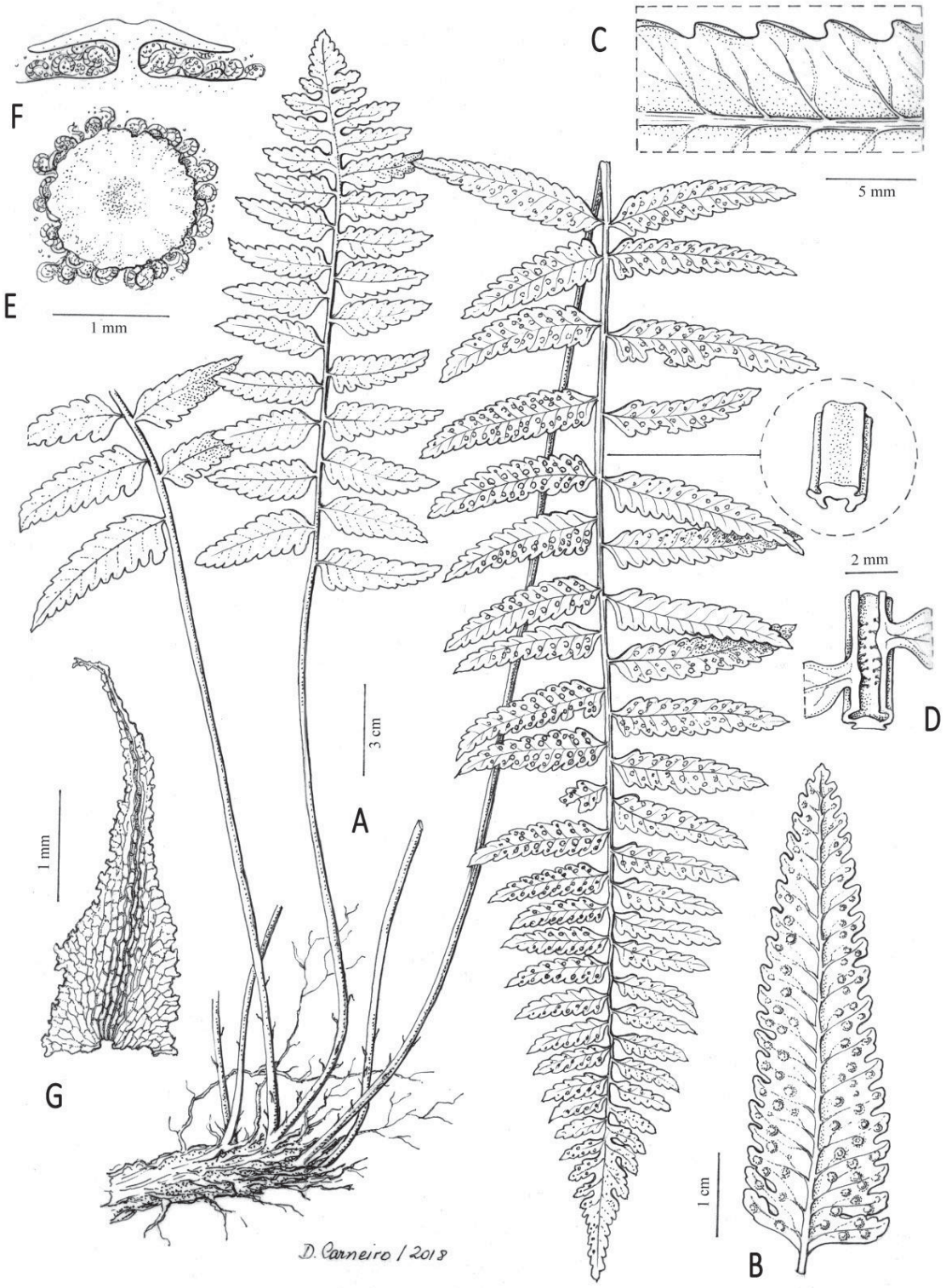


FIG. 6. *Cyclodium pubescens*. **A.** Habit of sterile frond with detail of anastomoses and pubescence of rachis. **B.** Rhizome scales. **C.** Petiole scales. **D.** Fertile frond with detail of pubescence of costa abaxially and laminar surface. **E.** Indusium. (A–E from *M. E. Engels 4763*, MBM).

Fig. 7. Spores of *Cyclodium.* **A.** *C. akawaiorum* (*Henkel et al. 4269,* NY). **B.** *C. alansmithii* (*Zartman et al. 9172*, INPA). **C.** *C. calophyllum* (*Liesner & González 13307*, UC). **D.** *C. chocoense* (*Hoover et al. 3935*, UC). **E.** *C. guianense* (*Costa 33*, UPCB). **F.** Differences in echinulated perine from two spores of *C. guianense* (*Secco et al. 303*, NY). **G.** Spore from the group with small fronds of *C. guianense* (*Cremers et al. 9193*, INPA). **H.** *C. heterodon* var. *abbreviatum* (*Pietrobom 4207*, NY). **I.** *C. heterodon* var. *heterodon* (*Labiak et al. 4058*, UPCB). **J.** *C. inerme* (*Ingham & Ingham 33935*, NY). **K.** *C. meniscioides* var. *meniscioides* (*Zuquim et al. 355*, INPA). **L.** *C. meniscioides* var. *paludosum* (*García-Barriga 14347*, US). Scale bars = 10 μm.

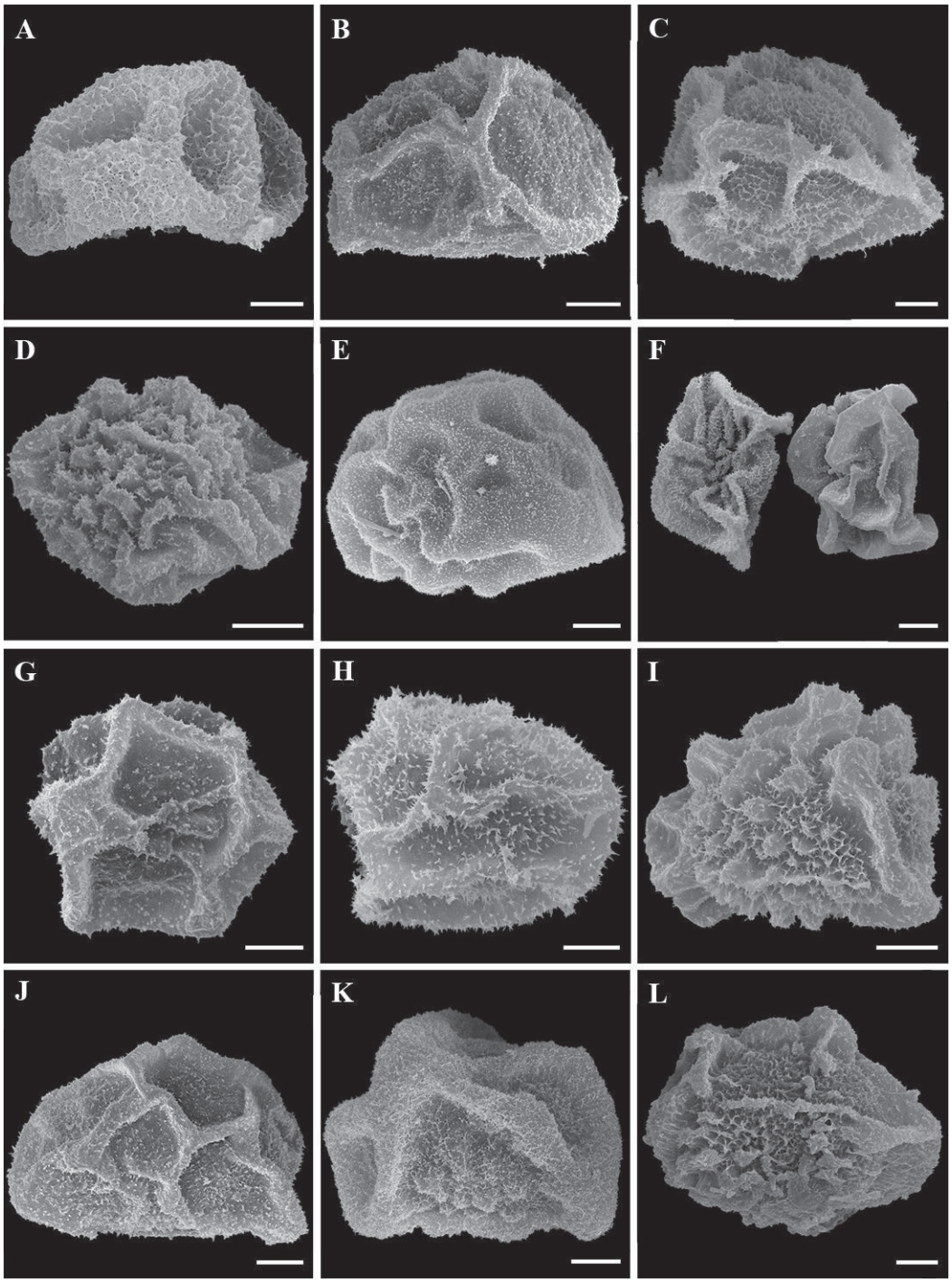
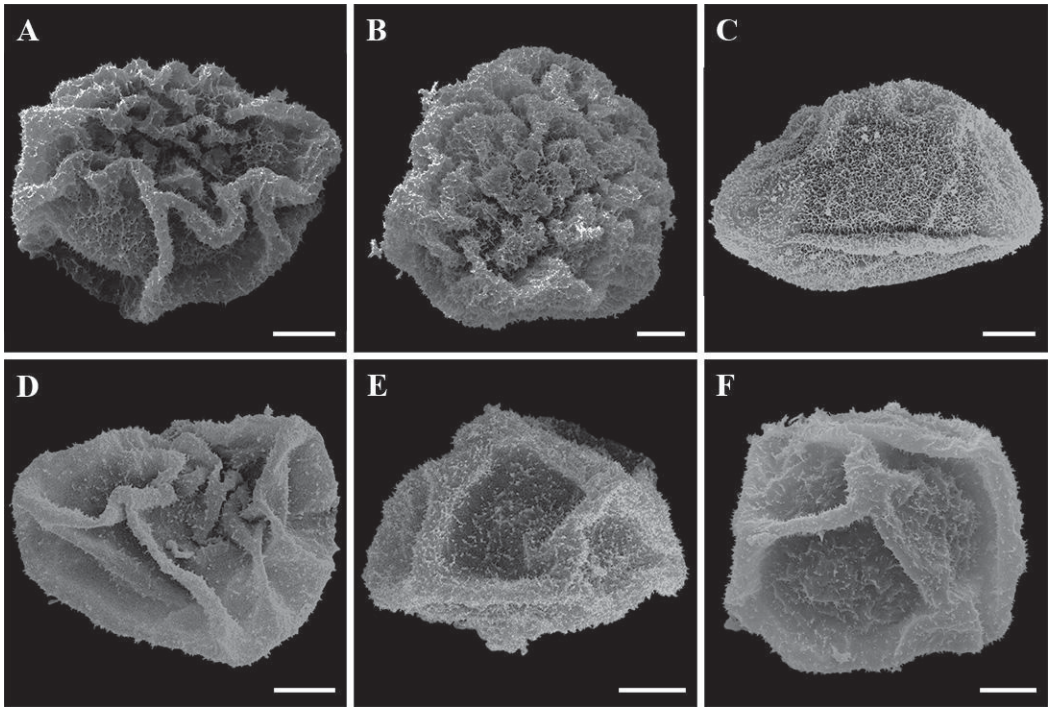


FIG. 8. Spores of *Cyclodium.* **A.** *C. meniscioides* var. *rigidissimum* (*Monteagudo & Francis 5309*, NY). **B.** *C. pubescens* (*Bronholi et al. 11-224,* UPCB). **C.** *C. rheophilum* (*Granville et al. 15523*, NY). **D.** *C. seemannii* (*Ramírez et al. 9611*, UC). **E.** *C. trianae* (*Rojas 0102*, NY). **F.** *C. varians* (*Clarke 10037*, NY). Scale bars = 10 μm.



Appendix 1

LIST OF ACCEPTED NAMES

1. *Cyclodium akawaiorum* A.R. Sm.

2. *Cyclodium alansmithii* Bohn & Labiak

3. *Cyclodium calophyllum* (C.V. Morton) A.R. Sm

4. *Cyclodium chocoense* (A.R.Sm.) Bohn & Labiak

5. *Cyclodium guianense* (Klotzsch) van der Werff ex L.D. Gómez

6. *Cyclodium heterodon* (Schrad.) T. Moore

7. *Cyclodium inerme* (Fée) A.R. Sm.

8. *Cyclodium meniscioides* (Willd.) C. Presl

9. *Cyclodium pubescens* Bohn & Labiak

10. *Cyclodium rheophilum* A.R. Sm.

11. *Cyclodium seemannii* (Hook.) A.R. Sm.

12. *Cyclodium trianae* (Mett.) A.R. Sm.

13. *Cyclodium varians* (Fée) A.R. Sm

LIST OF COLLECTOR'S NAMES AND NUMBERS

The numbers between parentheses refer to the corresponding species in the List of Accepted Names presented above. Accession numbers are given in brackets for species without a collection number.

Acevedo-Rodriguez, P.: 6807 (4)
Albánc, J.: 10016 (8)
Alberláez, A.: 198 (12); 248 (4)
Almeida, T. E.: 708, 2665, 2749, 4743 (8); 2012 (6); 2561 (12); 4176 (7)

Freitas, C. A. A.: 437 (9)
Froes, R. L.: 26025 (7)
Galdames, C.: 2432 (12)
García-Barriga, H.: 14347 (8)
Gardner, G.: 1218 (6)
Gentry, A.: 23937, 24057 (4)
Giacomin, L. L.: 1790 (5)
Gillespie, L. J.: 1523 (8); 2288 (2)
Glaziou, A.: 12373 (7); s.n. [P-01444020] (5)
Gleason, H. A.: 183 (8)
Gonçalves, K. S.: 130 (9)
Gonzáles, C.: 421, 497 (12)
Gonzalez, S.: 1752 (8)
Guedes, M. L.: 9390 (8)
Gueiros, R. A. G.: 180, 181 (8); 238, 239 (6)
Hagemann, W.: 424, 1702 (4)
Hahn, W.: 5424 (1)
Harley, R. M.: 17173 (6)
Hassler: 9049, 12969 (8)
Hatschbach, G.: 37462 (8); 51427 (6)
Haught, O.: 1353 (3)
Hawkins, T.: 1885 (5)
Henicka, G. S.: 293 (7)
Henkel, T. W.: 1222, 2174, 4106 (2); 1244, 1919 (8); 1372, 4269, 4321, 4349 (1); 4970, 5034 (5); 5723 (7)
Hequet, V.: 931 (7)
Heringer, G.: 13342 (6)
Herrera, H.: 339 (12)
Hitchcock, A. S.: 17124 (8)
Hoff, M.: 5918, 6719 (7) 7038 (8)
Hoffman, B.: 610, 887, 2678 (8); 2109, 2248 (2)
Holst, B. K.: 2573 (8); 2643 (13)
Hoover, W. S.: 3935 (4)
Householder, J. E.: 2935 (8)
Ingham, R.: 33935 (7)
Irwin, H. S.: 54523 (7)
Jangoux, J.: 85-34 (5)
Jansen-Jacobs, M. J.: 1507, 6799, 6882 (7); 4924, 6892 (8)
Jardim, A.: 2453 (8)
Jardim, J. G.: 2853, 4843 (8); 3010 (6)
Jenman, G. S.: s.n. [NY-02859579], s.n. [NY-02859621] (8); s/n [NY-02859616], s.n. [NY-02859617], s/n [NY-02859618], s/n [NY-02859623], s/n [NY-02859624] (13); s.n. [NY-2859535] (7)
Jiménez, I.: 1987, 1999 (8)
Kellof, C. L.: 860 (8)
Kessler, M.: 10967 (8)
Killip, E. P.: 28540 (12); 30335 (7); 33172, 33246, 33320, 33622, 35084, 35287, 38991 (4)
Kral, R.: 71864 (5)
Kramer, K. U.: 79 (7)
Krukoff, B. A.: 4924 (8)

3 CONSIDERAÇÕES FINAIS

Através dos resultados obtidos, é possível fazer algumas novas constatações sobre *Cyclodium.* Produzimos árvores filogenéticas através de dados moleculares de cinco marcadores de cloroplasto. Com respeito às relações do gênero com outros táxons de Dryopteridaceae, nossos resultados corroboram com a literatura já disponível. *Cyclodium* foi resolvido como monofilético e grupo irmão de *Polybotrya*, morfologicamente suportado pela sinpomorfia de possuir indúsio peltado, e o clado polibotrióide – o qual *Cyclodium* faz parte – é suportado pela presença de perina densamente equinulada. Apesar disso, *Polystichopsis* e seu grupo irmão *Trichoneuron*, foram considerados integrantes do clado polisticopsióide, como indicado em um estudo anterior.

Dos oito táxons de *Cyclodium* avaliados quanto à monofilia, seis são monofiléticos: *C. calophyllum, C. heterodon, C. inerme, C. meniscioides, C. trianae* var. *trianae* e *C. trianae* var. *chocoense.* A partir destes resultados, propusemos algumas modificações taxonômicas importantes: a proposição de uma nova espécie, *Cyclodium alansmithii* Bohn & Labiak (Capítulo 2), grupo irmão de *C. inerme* e morfologicamente muito semelhante; a mudança do status de *C. trianae* var. *chocoense* para a espécie *C. chocoense* (Capítulo 2) e a sinonimização de *C. heterodon* var. *abbreviatum* em *C. heterodon* (Capítulo 3) foram suportadas por evidências filogenéticas, morfológicas e geográficas. Com estes novos estabelecimentos, sugerimos algumas sinapomorfias: a ausência de escamas abaxiais na costa suporta o clado de *C. inerme* e *C. alansmithii;* o dimorfismo das frondes estéreis e férteis e a presença de ápice conforme suportam o clado de *C. akawaiorum* e *C. meniscioides*; e a presença de perfurações na perina do esporo é uma sinapomorfia para o clado de *C. heterodon, C. alansmithii, C. inerme, C. akawaiorum, C. meniscioides, C. guianense* and *C. rheophilum*, mas houve uma reversão deste estado para não perfurado em *C. inerme* e *C. guianense*.

Por fim, foram reconhecidas 13 espécies de *Cyclodium,* sem inclusão de variedades ou subespécies. A revisão taxonômica inclui todas as alterações taxonômicas já citadas, além da a proposição de uma segunda espécie nova, *Cyclodium pubescens*, similar à *C. meniscioides*, e difererindo desta pela densa presença de tricomas aciculares, eretos, translúcidos na raque, costa e tecido laminar. Através de uma consulta extensiva de materiais de herbário, consideramos que os caracteres morfológicos utilizados para separar as variedades de *C. meniscioides* (var. *paludosum* e var. *rigidissimum*) ocorrem em diversos espécimes, porém não foi possível identificar um padrão de ocorrência. Deste modo, estas

variedades foram sinonimizadas em *C. meniscioides*. Os cabeçalhos taxonômicos, descrições, mapas de distribuição, status de conservação, notas, coleções examinadas, pranchas de ilustrações, e lista de coletores são disponibilizadas. Além da chave dicotômica para as espécies de nervuras livres (Capítulo 2), este trabalho propõe uma segunda chave de identificação incluindo todas as espécies de *Cyclodium* (Capítulo 3).

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